Universidad de Alcalá

COMISIÓN DE ESTUDIOS OFICIALES DE POSGRADO Y DOCTORADO

ACTA DE EVALUACIÓN DE LA TESIS DOCTORAL

Año académico 2016/17

DOCTORANDO: **ARENAS ESCRIBANO, JUAN MARÍA** D.N.I./PASAPORTE: ******8328F**

PROGRAMA DE DOCTORADO: **D330 DOCTORADO EN ECOLOGÍA. CONSERVACIÓN Y RESTAURACIÓN DE ECOSISTEMAS**
DEPARTAMENTO DE: **CIENCIAS DE LA VIDA**
TITULACIÓN DE DOCTOR EN: **DOCTOR/A POR LA UNIVERSIDAD DE ALCALÁ**

En el día de hoy 19/07/17, reunido el tribunal de evaluación nombrado por la Comisión de Estudios Oficiales de Posgrado y Doctorado de la Universidad y constituido por los miembros que suscriben la presente Acta, el aspirante defendió su Tesis Doctoral, elaborada bajo la dirección de MIGUEL ÁNNGEL CASADO GONZÁLEZ // LUIS BALAGUER NÚÑEZ
ADRIÁN ESCUDERO ALCÁNTARA.

Sobre el siguiente tema: *VEGETACIÓN PERENNE EN TALUDES DE CARRETERA: CONDICIONANTES PARA SU ESTABLECIMIENTO Y OPORTUNIDADES PARA LA CONSERVACIÓN Y RESTAURACIÓN DE ECOSISTEMAS*

Finalizada la defensa y discusión de la tesis, el tribunal acordó otorgar la CALIFICACIÓN GLOBAL[1] de (**no apto, aprobado, notable y sobresaliente**): _SOBRESALIENTE_

Alcalá de Henares, _19_ de _JULIO_ de _2017_

EL PRESIDENTE   EL SECRETARIO   EL VOCAL

Fdo.: _FERNANDO VALLADARES ROS_   Fdo.: _JOSÉ Mª REY BENAYAS_   Fdo.: _PATRICIO GARCÍA-FAYOS POVEDA_

Con fecha _21_ de _julio_ de _2017_ la Comisión Delegada de la Comisión de Estudios Oficiales de Posgrado, a la vista de los votos emitidos de manera anónima por el tribunal que ha juzgado la tesis, resuelve:

☒ Conceder la Mención de "Cum Laude"
☐ No conceder la Mención de "Cum Laude"

La Secretaria de la Comisión Delegada

FIRMA DEL ALUMNO,

Fdo.: _JUAN M. ARENAS ESCRIBANO_

[1] La calificación podrá ser "no apto" "aprobado" "notable" y "sobresaliente". El tribunal podrá otorgar la mención de "cum laude" si la calificación global es de sobresaliente y se emite en tal sentido el voto secreto positivo por unanimidad.

INCIDENCIAS / OBSERVACIONES:

En aplicación del art. 14.7 del RD. 99/2011 y el art. 14 del Reglamento de Elaboración, Autorización y Defensa de la Tesis Doctoral, la Comisión Delegada de la Comisión de Estudios Oficiales de Posgrado y Doctorado, en sesión pública de fecha 24 de julio, procedió al escrutinio de los votos emitidos por los miembros del tribunal de la tesis defendida por *ARENAS ESCRIBANO, JUAN MARÍA*, el día 19 de julio de 2017, titulada *VEGETACIÓN PERENNE EN TALUDES DE CARRETERA: CONDICIONANTES PARA SU ESTABLECIMIENTO Y OPORTUNIDADES PARA LA CONSERVACIÓN Y RESTAURACIÓN DE ECOSISTEMAS*, para determinar, si a la misma, se le concede la mención "cum laude", arrojando como resultado el voto favorable de todos los miembros del tribunal.

Por lo tanto, la Comisión de Estudios Oficiales de Posgrado **resuelve otorgar** a dicha tesis la

MENCIÓN "CUM LAUDE"

Alcalá de Henares, 27 julio de 2017
EL PRESIDENTE DE LA COMISIÓN DE ESTUDIOS
OFICIALES DE POSGRADO Y DOCTORADO

Firmado digitalmente por VELASCO
PEREZ JUAN RAMON - DNI
03087239H
Fecha: 2017.07.28 11:11:22 -06'00'

Juan Ramón Velasco Pérez

Copia por e-mail a:
Doctorando: ARENAS ESCRIBANO, JUAN MARÍA
Secretario del Tribunal: JOSÉ MARÍA REY BENAYAS.
Directores de Tesis: MIGUEL ÁNGEL CASADO GONZÁLEZ // LUIS BALAGUER NÚÑEZ // ADRIÁN ESCUDERO ALCÁNTARA

DILIGENCIA DE DEPÓSITO DE TESIS.

Comprobado que el expediente académico de D./Dª _____ reúne los requisitos exigidos para la presentación de la Tesis, de acuerdo a la normativa vigente, y habiendo presentado la misma en formato: ☐ soporte electrónico ☐ impreso en papel, para el depósito de la misma, en el Servicio de Estudios Oficiales de Posgrado, con el nº de páginas: _____ se procede, con fecha de hoy a registrar el depósito de la tesis.

Alcalá de Henares a _____ de _____ de 20_____

MARTA VEGA

Fdo. El Funcionario

Universidad
de Alcalá

Vegetación perenne en taludes de carretera:
Condicionantes para su establecimiento
y oportunidades para la conservación
y restauración de ecosistemas

Juan María Arenas Escribano

Universidad Complutense
Departamento interuniversitario de Ecología
Facultad de Biología 28040-Madrid, España
Tno. +34 91 394 5123, +34 91 394 5086 ; Fax +34 91 394 5081

Miguel Ángel Casado
mcasado@ucm.es

Miguel Ángel Casado González, *profesor Titular de Ecología en el Departamento de Ecología de la Universidad Complutense de Madrid,* y Director/codirector de la presente Tesis doctoral ,

HACE CONSTAR:

Que el trabajo descrito en la presente memoria, titulado "**Vegetación perenne en taludes de carretera: Condicionantes para su establecimiento y oportunidades para la conservación y restauración de ecosistemas**", ha sido realizado bajo mi dirección por D. **Juan María Arenas Escribano** dentro del Programa de Doctorado de Ecología, Conservación y Restauración de Ecosistemas (D330), adscrito al Departamento de Ciencias de la Vida, de la Universidad de Alcalá. Esta tesis reúne todos los requisitos propios de este tipo de trabajo: rigor científico, aportaciones novedosas y aplicación de una metodología adecuada. Por lo tanto, doy mi Visto Bueno a la presentación de dicha Tesis Doctoral.

Madrid, 20 de Abril de 2017

Universidad Complutense
Departamento interuniversitario de Ecología
Facultad de Biología 28040-Madrid, España
Tno. +34 91 394 5123, +34 91 394 5086 ; Fax +34 91 394 5081

Miguel Ángel Casado
mcasado@ucm.es

Luís Balaguer Núñez, Profesor Titular en el Departamento de Biología Vegetal I de la Universidad Complutense de Madrid, director de la presente Tesis Doctoral, falleció en Madrid el 19 de marzo de 2014. Por lo tanto, yo, **Miguel Ángel Casado González** como director de la presente tesis, **hago constar que:**

El profesor Balaguer dirigió junto a mi la presente Tesis Doctoral hasta el momento de su fallecimiento, participando activamente en todas las fases de la misma. Luis confió en la capacidad de Juan María Arenas para llevar a cabo cada uno de los trabajos que se desarrollan en ésta tesis y mantuvo la ilusión y la certeza de que ésta tesis alcanzaría la calidad suficiente para superar con éxito la etapa de defensa. Sin duda, ésta tesis no habría sido posible sin su perspectiva de futuro, su ilusión y su constante apoyo científico, por lo que solicito que se mantenga como co-director de la misma.

Madrid, 20 de Abril de 2017

Universidad Rey Juan Carlos

Adrián Escudero Ancántara, *catedrático de Ecología de la URJC,* y Director/codirector de la presente Tesis doctoral ,

HACE CONSTAR:

Que el trabajo descrito en la presente memoria, titulado "**Vegetación perenne en taludes de carretera: Condicionantes para su establecimiento y oportunidades para la conservación y restauración de ecosistemas**", ha sido realizado bajo su dirección por D. **Juan María Arenas Escribano** dentro del Programa de Doctorado de Ecología, Conservación y Restauración de Ecosistemas (D330), adscrito al Departamento de Ciencias de la Vida, de la Universidad de Alcalá. Esta tesis reúne todos los requisitos propios de este tipo de trabajo: rigor científico, aportaciones novedosas y aplicación de una metodología adecuada. Por lo tanto, doy mi Visto Bueno a la presentación de dicha Tesis Doctoral.

Mostoles, 20 de Abril de 2017

Universidad de Alcalá

**DEPARTAMENTO DE
CIENCIAS DE LA VIDA**
Edificio de Ciencias
Campus Universitario
28805 Alcalá de Henares
(Madrid)
Telf. +34 918854927
E-mail: dpto.ccvida@uah.es

UNIVERSIDAD DE ALCALÁ. PATRIMONIO DE LA HUMANIDAD

LUISA DÍAZ ARANDA, Profesora Titular y Directora en funciones del Departamento de Ciencias de la Vida de la Universidad de Alcalá,

INFORMA:

Que el trabajo descrito en la presente memoria, titulado **"Vegetación perenne en taludes de carretera: Condicionantes para su establecimiento y oportunidades para la conservación y restauración de ecosistemas"**, ha sido realizado por D. Juan María Arenas Escribano dentro del Programa de Doctorado Ecología. Conservación y Restauración de ecosistemas (D330), reúne todos los requisitos necesarios para su aprobación como Tesis doctoral, por acuerdo del Consejo de Departamento celebrado el día 26 de abril de 2017

Alcalá de Henares, 26 de abril de 2017

Universidad de Alcalá

Vegetación perenne en taludes de carretera: Condicionantes para su establecimiento y oportunidades para la conservación y restauración de ecosistemas

Juan María Arenas Escribano

Programa de Doctorado de Ecología, Conservación y Restauración de Ecosistemas (D330)

Fotografías: Miguel Ángel Casado e Iñaki Mola
Diseño y maquetación: Alberto Martínez Martín

A mis directores: Miguel, Adri, y como no a Luis.
A mis padres,
a Klara
y a Gael

ÍNDICE

Vegetación perenne en taludes de carretera: Condicionantes para su establecimiento y oportunidades para la conservación y restauración de ecosistemas

---

CAPÍTULO 6
Discusión general   *99*

CONCLUSIONES GENERALES   106

Capítulo 1

Introducción general: Contexto y coherencia para la tesis

CONTEXTO GLOBAL

Impactos de la construcción carreteras

El 50% de la superficie terrestre está afectada por actividades humanas que implican movimientos de tierras o modificaciones en el flujo de sedimentos (Vitousek et al. 1997; Hooke et al. 2012). De entre estas actividades, humanas un 0,4% corresponde a carreteras en áreas rurales (ver Tabla 1 en Hooke et al., 2012). Igualmente, Forman (2000) estimó que la red de carreteras ocupa alrededor del 1% del territorio en países desarrollados, valor que coincide con el estimado para España (Balaguer et al. 2011). Esta extensa red de carreteras es responsable de un conjunto de impactos directos asociados a su construcción que afectan a ese 1% del territorio. El impacto más evidente es la propia ocupación del espacio por la propia vía. Además, en las carreteras construidas en las ultimas décadas se intenta que tengan la menor pendiente posible, adaptando el terreno a la carretera y no al revés, como se había venido haciendo de forma tradicional, por lo que para salvar los desniveles se generan grandes taludes. Por un lado se crean terraplenes, que son construidos por acopio de materiales para asentar encima la vía. Por otro lado desmontes, que son excavaciones o cortes en el terreno para bajar la cota. Ambos tipos de taludes dejan zonas desprovistas tanto de vegetación como de suelo. Por último, debido a los trabajos de construcción, en las zonas contiguas a la vía se produce una fuerte degradación del suelo, así como la eliminación de mucha de la vegetación.

Junto a estos impactos directos derivados de la construcción de la vía, el área ecológicamente afectada por la red de carreteras es mucho más amplia que el área físicamente modificada, llegando a modificar entre el 15% y el 20% del territorio de Estados Unidos (Forman & Alexander 1998; Forman 2000). Cuando se habla de impactos ecológicos de las carreteras, tradicionalmente se hace referencia a los impactos negativos que estas producen (Trombulak & Frissell 2000). Así, las carreteras provocan mortandad de individuos por atropellos, modifican el comportamiento de especies que no se acercan a la vía y provocan el aislamiento de poblaciones por un efecto de fragmentación y barrera (Fu et al. 2010). Estos efectos sobre los animales son sobre toda la comunidad, ya que hay especies que necesitan de esos movimientos para conectar poblaciones aisladas, dispersarse, etc. Pero además las carreteras también provocan alteraciones en el ambiente físico-químico cercano a la vía, tanto por cambios en flujos de agua y sedimentos (Coffin 2007), como por la deposición de contaminantes. Por último, se ha descrito que los márgenes de carretera pueden ser una vía para la dispersión de especies invasoras (Gelbard & Belnap 2003; Maheu-Giroux & Blois 2006).

No poniendo en duda la efectos adversos de las carreteras sobre el ecosistema, en los últimos años diversos autores están planteando que los márgenes de carretera pueden, en algunos casos, servir para mejorar la conservación de la biodiversidad y fortalecer algunos servicios ecosistémicos debilitados, especialmente servicios de soporte y de regulación, en ecosistemas agrícolas fragmentados y/o de intensificación agraria. Los ecosistemas agrícolas fragmentados están formado por parches o remanentes de hábitat (*sensu* Saunders et al. 1991) embebidos en una matriz agrícola. Los efectos negativos de la fragmentación sobre las comunidades de estos remanentes se relacionan principalmente con el tamaño de los mismos y con su aislamiento o conectividad (Turner 1996; Harrison 1999; Bruun 2000; Debinski & Holt 2000). En remanentes pequeños, las poblaciones sufren los efectos negativos asociados a poblaciones pequeñas, con el consiguiente riesgo de extinción local. Este efecto puede mitigarse, en parte, si la conectividad de los fragmentos pequeños es alta (Rösch et al. 2013). Por otro lado, la intensificación agraria ha provocado una homogeneización de los ecosistemas, debido a la pérdida de rotación de cultivos y a la eliminación de lindes, barbechos y tierras marginales, lo que deriva en una

perdida de conectividad y de biodiversidad, y por tanto, de servicios ecosistémicos a todos los niveles (Benton et al. 2003; Karp et al. 2012).

En este contexto de intensificación de los usos del suelo, los potenciales efectos positivos de las carreteras se basan en dos conceptos. Por un lado, los márgenes de las carreteras son zonas libres de cultivo, donde se pueden establecer comunidades duraderas y hacer frente a la homogeneización provocada por la intensificación agraria. Estas comunidades pueden ser un refugio de biodiversidad (Tikka et al. 2000; Spooner & Smallbone 2009), lo cual aporta, entre otros, los siguiente beneficios directos: 1) Mantener especies amenazadas o singulares que están en peligro por la desaparición de los fragmentos de vegetación natural en los entornos agrícolas intensivos. De hecho, en algunos estados de Australia ya se ha trabajado en "road reserves" (reservas de carretera) para proteger una flora que ha desaparecido de gran parte del territorio y que queda recluida en los márgenes de las carreteras (Spooner & Smallbone 2009); 2) Albergar especies parientes de variedades cultivadas (Jarvis et al. 2015), lo que supone una reserva genética adaptada al entorno de cara a cambios en las condiciones que requieran nuevas variedades (plagas, cambios climático, etc.); 3) Ser una reserva de especies como fuente de propágulos para posteriores restauraciones pasivas de campos abandonado, y 4) Ofrecer refugio y oportunidad para completar su ciclo vital a polinizadores y depredadores, lo que deriva en una mejora de los cultivos por aumentos en la polinización y el control de plaga (Wynhoff et al. 2010; Noordijk et al. 2011). Por otro lado, en los márgenes de carretera se ha demostrado la existencia tanto de flujos de especies paralelos a la vía (Tikka et al. 2001) como de flujos perpendiculares que conectan estos ecosistemas emergentes con la vegetación cercan (Lugo & Gucinski 2000). La existencia de ambos tipos de flujos puede aumentar la conectividad entre remanentes de hábitat, lo que reduce el impacto provocado por la fragmentación agrícola. En esta función de canalizador de flujos y

mejora de la conectividad, los márgenes de carreteras pueden actuar como corredores biológicos (Tikka et al. 2001), como nodos y conexiones de metapoblacionales e incluso, como rutas migratorias.

Restauración de los márgenes de carretera

Los márgenes de carretera, ya sean los construidos por acopio de materiales, por excavación o las áreas degradadas por las propias actividades de construcción de la vía, son zonas desprovistas de vegetación y de suelo en sus primeros momentos. Las zonas con pendiente (desmontes y terraplenes) necesitan una restauración a corto plazo centrada en controlar la erosión de los taludes. Controlar la erosión de desmontes y terraplenes es necesario para garantizar la estabilidad de la carretera y para reducir los sedimentos que llegan tanto a la propia vía como a las cunetas, zonas de drenaje de agua, etc. Dada la ausencia de un suelo desarrollado estos hábitats representan unos filtros abióticos muy importantes para ser colonizados, los cuales se agravan en el clima mediterráneo (clima en el que se enmarcan los estudios experimentales de esta tesis), caracterizado por veranos muy secos y cálidos (Aschmann 1973). Estas condiciones abióticas tan duras y la necesidad de conseguir una cubierta vegetal en un corto plazo de tiempo para limitar la erosión, obliga a realizar sobre los taludes restauraciones técnicas (Prach & Hobbs 2008). Las técnicas actuales de restauración se suelen basar en el extendido de tierra vegetal, hidrosiembra con plantas herbáceas comerciales de rápido crecimiento (Mola et al. 2011) y en algunos casos, plantaciones de especies leñosas.

Frente a estas medidas cortoplacistas y focalizadas en los taludes, la restauración ecológica de los márgenes de carreteras para mejorar la conservación de la biodiversidad y fortalecer algunos servicios ecosistémicos debilitados tiene que marcarse objetivos a medio y largo plazo. Las restauraciones a largo plazo necesitan indudablemente contar con la restauración pasiva o colonización natural de los taludes, ya que

como apuntaron Prach & Hobbs (2008), dicha colonización natural tiene muchas ventajas sobre las restauraciones técnicas: 1) Las especies están adaptadas a las condiciones locales y por tanto no necesitan mantenimiento (Kovář 2004); 2) El valor natural de los sitios colonizados espontáneamente es generalmente mayor que el de los sitios con restauraciones técnicas (Hodačová & Prach 2003); 3) Las diferentes etapas de sucesión proporcionan refugios para la vida silvestre, etapas que se pierden con las restauraciones técnicas y 4) Por ultimo y no menos importante en nuestro contesto, la colonización natural es mucho más barata.

Sin embargo, la colonización natural puede estar profundamente influenciada por las actividades de restauración, control y manejo que se realizan habitualmente en los márgenes de las carreteras. El principal problema derivado de las restauraciones técnicas es el posible secuestro de la sucesión provocado por el interés de favorecer una rápida cubierta vegetal en los taludes. Entre las medidas de gestión que pueden dificultar la sucesión natural están la retirada de sedimentos en las zonas de acumulación, las siegas y quemas controladas de la vegetación, e incluso el reperfilado de taludes. Estas actividades se realizan siempre con unos objetivos técnicos a corto plazo, como son la reducción de las zonas de acumulación de sedimentos en las cunetas para mejorar el drenaje del agua tras las lluvias y la eliminación de la vegetación para aumentar la seguridad vial y evitar incendios en verano. Estos objetivos a corto plazo de la restauración técnica y de la gestión pueden entrar en conflicto con objetivos planteados a medio y largo plazo (Holl 2002). Por tanto, es necesario hacer un esfuerzo en los planes de restauración para proponer objetivos integrados a diferentes escalas temporales y espaciales (Parker 1997). Este esfuerzo debe combinar la necesidad de los gestores de las carreteras de mantener la integridad y seguridad de la vía junto con los objetivos a largo plazo centrados en promover la colonización natural de los taludes, como paso previo para potenciar la conservación de la biodiversidad y el fortalecimiento de servicios ecosistémicos.

MARCO CONCEPTUAL

El planteamiento de esta tesis permite profundizar en la base de conocimientos que permita desarrollar medidas de restauración y gestión de los márgenes de carretera con objetivos a medio y largo plazo, como pueden ser la conservación de la biodiversidad o el fortalecimiento de los servicios ecosistémicos debilitados. Para ello el trabajo realizado se ha focalizado en la vegetación perenne y los estudios se han planteado a escalas amplias. Este planteamiento ha permitido conocer los condicionantes para el establecimiento de la vegetación perenne en márgenes de carretera y analizar las potencialidades de dichos márgenes en la oferta de servicios ecosistémicos en un entornos fragmentado y de alto interés para la conservación.

Importancia del estudio de vegetación leñosa y perenne en taludes

La vegetación perenne es parte fundamental en la mayoría de los ecosistemas terrestres. De hecho, se ha descrito como ingeniera del paisaje (Jones et al. 1994), facilitando el establecimiento de otras especies por la mejora de algunos condicionantes abióticos, como disponibilidad de nutrientes, agua y microclima, especialmente en climas estresantes como el Mediterráneo (Bruno et al. 2003; Perelman et al. 2003; Gómez-Aparicio et al. 2004; Wilby & Shachak 2004; Luzuriaga et al. 2012). Además, Rey Benayas y colaboradores (2008) apuntaron a que la vegetación arbórea en ambientes degradados es atractora de especies animales y con ello aumenta la posibilidad de llegada de semillas y aumenta la conectividad entre parches de vegetación. No obstante, en este punto hay controversia, ya que algunos estudios apuntan a que los efectos atractores que comentan Rey Benayas y colaboradores (2008) son muy dependientes del paisaje circundante, que es a la postre de donde provienen las especies dispersoras (de Torre et al. 2015).

Además, el estudio de la vegetación perenne permite obtener conclusiones no dependientes de momentos concretos (picos fenológicos, cambios meteorológicos interanuales, etc.). Así mismo, las relaciones abióticas (facilitación, competición, etc.) entre especies son más estables en el tiempo y permanecen a lo largo de los años. Esto, junto a la importancia de la vegetación en los ecosistemas mediterráneos, hace que los objetivos de la restauración ecológica a largo plazo tengan que focalizarse, al menos en parte, en dicho tipo de vegetación.

La presencia de vegetación leñosa en los taludes se debe principalmente a dos procesos. Por un lado, a las plantaciones realizadas en algunos taludes como medida de restauración. Estas plantaciones son realizadas en la mayor parte de los casos para mejorar la estabilidad geomorfológica de los taludes y con fines estéticos, aunque también se les atribuye unas potencialidades para la integración ecológica (García-Palacios et al. 2011), aunque de dudosa efectividad (de Torre et al. 2015). Las plantaciones son relativamente caras para las empresas y tienen el problema de que no están adaptadas a las condiciones locales extremas que se dan en los taludes tras su construcción (Hartley 2002). Por otro lado, la vegetación perenne puede llegar a los taludes y establecerse mediante colonización natural.

Pese al importante papel que puede jugar la vegetación perenne hay pocos estudios que centren su estudio en este tipo de plantas en márgenes de carretera en ambientes mediterráneos. Frente a esta falta de información los cuatro capítulos que conforman la presente tesis se centran exclusivamente en la vegetación perenne. En dos capítulos se tratan de conocer los procesos que rigen la colonización natural y el establecimiento de la vegetación leñosa en taludes de carretera, un tercer capítulo plantea el estudio de las similitudes y diferencias de las comunidades de plantas perennes (leñosas y herbáceas) del entorno y las de los márgenes de carretera, así como los factores que rigen la presencia de dicha vegetación en los márgenes. El último capítulo experimental está enfocado a conocer los factores que determinan la comunidad de plantas perennes de remanentes de hábitats en un ecosistema atravesado por una autovía.

Condicionantes para la colonización de márgenes de carretera

La colonización de un hábitat de nueva creación, como los taludes de carretera, tiene dos principales limitaciones: la llegada de semillas y la disponibilidad de un micrositio idóneo para su establecimiento (Münzbergová & Herben 2005). Las técnicas utilizadas en la restauración de taludes pretenden romper estas limitaciones. La llegada de semillas se intenta mejorar mediante el banco de semillas de la tierra vegetal y las hidrosiembras, y en menor medida con plantaciones. Sin embargo, se ha demostrado que el banco de semillas en la tierra vegetal utilizada en taludes de carretera es muy pobre (Dickie et al. 1988; Mola et al. 2011). Mola y colaboradores (2011) también demostraron que la lluvia de semillas aporta hasta siete veces más semillas en un año que las hidrosiembras. Esto implica que la mayoría de las semillas llegan a los taludes desde el entorno, como también han demostrado otros autores (Bochet et al. 2007; de la Riva et al. 2011). De estas especies que llegan a los taludes, las especies herbáceas anemócoras están sobrerrepresentadas, al menos en los primeros años tras la construcción de los taludes (Bochet et al. 2007). Por otro lado, los distintos vectores responsables de la dispersión de las semillas pueden condicionar la cantidad y tipo de especies que llegan a un territorio. Se ha planteado que las especies dispersadas por aves son especialmente importantes para la restauración de espacios degradados (Bonet 2004; Méndez et al. 2008; García et al. 2010). Sin embargo, la efectividad de la dispersión de estas especies zoócoras depende tanto de la existencia de fuentes apropiadas de semillas como de la actividad de sus dispersores (Jordano & Godoy 2002). Los nuevos taludes en general no son muy atractivos para la fauna dispersora de semillas (Cuperus et al. 1996; Verdú & García-Fayos 1996; de Torre et al. 2015), por lo que la entrada de especies

zoócoras suele ser lenta. Además de los propios vectores de dispersión (viento o animales), la configuración del paisaje es clave para determinar la llegada de semillas a los taludes desde el entorno. En el caso de las especies anemócoras, la llegada de semillas puede verse modificada por cambios en la velocidad y dirección del viento producidos por la presencia, disposición y densidad de las zonas arboladas (Nathan et al. 2002; Bohrer et al. 2008; Pounden et al. 2008; Schurr et al. 2008). Para las especies zoócoras, la calidad del hábitat de los remanentes define tanto la cantidad de semillas disponibles como la abundancia de las especies dispersoras (García et al. 2010; de Torre et al. 2015).

En climas mediterráneos la llegada de semillas a los márgenes de carretera no es suficiente para asegurar la germinación y el establecimiento (Tormo et al. 2006). Esto se debe a que las especies tienen que atravesar unos filtros importantes a nivel de micrositio (Münzbergová & Herben 2005), entre ellos: la disponibilidad de agua y el estrés hídrico (Bochet et al. 2007; Tormo et al. 2008); la baja cantidad de nutrientes y materia orgánica (Mola et al. 2011; Jiménez et al. 2011); parámetros físico-químicos, como la compactación del suelo o la falta de estructura (Jim 1998); las condiciones microclimáticas (Cano et al. 2002; de Torre 2014); e incluso las interacciones bióticas entre especies de plantas (García-Palacios et al. 2010; de la Riva et al. 2011) y entre planta y otros componentes vivos del suelo (García-Palacios et al. 2011). Todos estos condicionantes a escala de micrositio son dependientes de las características concretas de cada margen de carretera. Por tanto, los filtros que actúan en terraplenes y en desmontes pueden ser muy diferentes, debido a sus características constructivas (Bochet & García-Fayos 2004; Jiménez et al. 2011). La litología de la zona por la que atraviesa la carretera define los materiales con los que se construyen los terraplenes y los materiales que quedan expuestos tras las excavaciones para hacer los desmontes, lo que afecta principalmente a las características físico-químicas. La pendiente de los taludes tienen gran relación con la creación de zonas de erosión y acumulación de materiales, agua y nutrientes. Igualmente, la orientación afecta a las características microclimáticas (Cano et al. 2002). Las diferentes técnicas de restauración, como el extendido de tierra vegetal, tratan de reducir el efecto de algunos de estos filtros abióticos (Jiménez et al. 2011). A su vez, con el transcurso de los años desde la construcción de una carretera, por norma general el suelo va madurando y los filtros abióticos disminuyen su efecto (García-Palacios et al. 2011).

Pese a que muchos de estos condicionantes a escala de micositio son ya relativamente conocidos, no hay apenar estudios sobre su efecto en la colonización de la vegetación perenne en márgenes de carretera en clima Mediterráneo. En esta tesis se han planteado tres capítulos para comprender los procesos de colonización y desarrollo de la vegetación perenne en márgenes de carretera.

Importancia de los estudios en escalas amplias

La mayoría de los estudios en taludes de carretera han sido realizados con muy pocos taludes y en un área geográfica muy limitada. Sin embargo, muchos de los procesos en taludes han sido descritos como "site-dependent" (García-Palacios et al. 2010; de Torre 2014) y por tanto, los resultados son difícilmente extrapolables si el número de taludes estudiados no es muy grande (Prach et al. 2007). Además, los efectos de las factores que operan a escalas amplias, como el clima, los factores litológicos, los usos del suelo o la estructura del paisaje no pueden ser evaluados si no se planean investigaciones a escala regional, ya que las conclusiones sacadas a una escala local, no puede ser extrapoladas a escalas mayores (Lugo & Gucinski 2000; Novák & Prach 2003; Münzbergová 2004). Por otro lado, los potenciales efectos de los márgenes de carretera para la conservación de la biodiversidad y el fortalecimiento de los servicios ecosistémicos necesitan ser estudiados al menos a escala de paisaje, ya que dichos efectos deben superar

las inmediaciones de la vía y conectar distintos territorios para que realmente sean determinantes a escala de paisaje.

En esta tesis se han planteado dos estudios experimentales a escala regional amplia para poder emitir conclusiones generalizables sobre la colonización de vegetación leñosa en taludes de carretera. Los otros dos capítulos se plantean a escala de paisaje para conocer las potencialidades de los márgenes de carretera como refugios de biodiversidad y canalizadores de flujos de vegetación.

Paisajes agrícolas fragmentados: escenarios obligatorios para esta tesis

Los países industrializados han sufrido históricamente un fuerte proceso de fragmentación debido principalmente a las prácticas agrícolas, las cuales han transformado el paisaje en remanentes de vegetación natural de diferentes tamaños intercalados entre los cultivos (Saunders et al. 1991). Como ya se ha comentado previamente, márgenes de las carreteras pueden jugar un papel fundamental en la conservación de la biodiversidad y la recuperación de servicios ecosistémicos degradados en este tipo de paisajes fragmentados. Por tanto, todos los estudios de esta tesis se han llevado a cabo en dichos paisajes. Además, estos escenarios son idóneos para conocer la influencia de la estructura del paisaje en los procesos de colonización natural de los márgenes de las carreteras, ya que permiten estudiar ambientes contrastados, desde situaciones que mantienen muy cerca vegetación perenne y con altas coberturas, hasta los que están completamente rodeados de campos agrícolas.

En la presente tesis, dos capítulos han sido diseñados para conocer esta influencia del entorno en el proceso de colonización natural de los márgenes de carreteras, mientras que otros dos se han centrado en conocer las potencialidades de dichos márgenes para la mejora de la conservación y el aumento de servicios ecosistémicos en sistemas agrícolas fragmentados.

Paisaje agrícola fragmentado de interés para la conservación

Los servicios ecosistémicos y las posibilidades para la conservación de la biodiversidad que pueden ofrecer los márgenes de carretera en paisajes agrícolas fragmentados toman aun más relevancia si los remanentes de hábitat tienen especial interés para la conservación. Debido a ello, para los dos capítulo de esta tesis en los que más directamente se valoran los potenciales efectos positivos que podrían tener los márgenes de carretera sobre el ecosistema se ha seleccionado un paisaje agrícola fragmentado sobre una litología de yesos.

Los ecosistemas de yesos, debido a su rareza y a su singularidad, están protegidos a nivel europeo (Directiva de conservación de los hábitats naturales y de la fauna y flora silvestres; Directive 92/43/CEE, 1992), lo que ha derivado en el aumento de las figuras de protección de la flora de yesos a nivel regional y estatal (Moreno 2008). Los ecosistemas de yesos tradicionalmente se han considerado tierras marginales y por tanto han sido utilizadas para diversos usos, como reforestaciones o vertederos, degradando o eliminando con ello la vegetación natural de estos hábitats. Sin embargo, la vegetación gipsófila está fuertemente determinada por las especiales características de este tipo de suelos. Pero además, la fragmentación de su hábitat es uno de los principales factores que ponen en peligro a la vegetación gipsófila (Pueyo & Alados 2007; Pueyo et al. 2008). En esta línea, Pueyo y colaboradores (2008) apuntaron que las especies gipsófilas son más vulnerables a la fragmentación del territorio que las especies generalistas, aunque no pudieron determinar si esta vulnerabilidad era debida al efecto de aislamiento o a la propia degradación que sufren los fragmentos más pequeños. Además, aparte de la fragmentación *per se*, un ecosistema fragmentado sufre una gran perdida de hábitat disponible (Fahrig 2013), lo que redunda en una fuerte pérdida de comunidades y especies. Por todo ello, un paisaje fragmentado sobre un afloramiento de yesos es un buen escenario

para testear los posibles efectos positivos que pueden aportar los márgenes de carretera sobre una flora protegida a nivel europeo y estatal.

OBJETIVOS DE LA PRESENTE TESIS

Los objetivos generales de esta tesis son: a) conocer los mecanismos que determinan la colonización de taludes de carretera por parte de la vegetación leñosa, y b) conocer las potencialidades de los márgenes de carretera como refugio de vegetación perenne y como canalizadores de flujos de vegetación en un ambiente fragmentado pero de alto interés para la conservación. Para afrontar estos dos objetivos generales la tesis está estructurada en cuatro capítulos experimentales en los cuales se abordan objetivos más específicos que permiten, en último término, dar recomendaciones a las empresas y administraciones para la restauración y gestión de los márgenes de carreteras con una visión a medio y largo plazo. Cada uno de esos cuatro capítulos corresponde a un artículo científico publicado o en vías de publicación en revistas SCI.

El **Capítulo 2** plantea un estudio a nivel regional amplio (toda la Comunidad de Madrid) de los factores que determinan la presencia de vegetación leñosa en los terraplenes de las autovías y autopistas. El estudio incluye variables tanto a escala local y de paisaje (talud y entorno) como a escala regional (variabilidad climática, geográfica y de usos del suelo). El objetivo de esta capítulo es describir los patrones de establecimiento de la vegetación leñosa de gran porte en terraplenes sobre un territorio amplio y ambientalmente heterogéneo, y analizar su relación con factores que actúan a escala geográfica regional o local. Con este planteamiento se trata de responder a las siguientes preguntas concretas: 1) ¿Hasta qué punto la presencia de plantas leñosas plantadas influye en los patrones de reclutamiento natural en los bordes de las carreteras? 2) ¿Cuáles son los factores clave (los propios del talud, los entornos o factores que actúan a escala regional) que influyen en

el reclutamiento de plantas leñosas en los márgenes de las carreteras?

Los resultados del Capítulo 2 han permitido resaltar algunos patrones generales aplicables a grandes territorios ambientalmente heterogéneos (toda la Comunidad de Madrid). Estos resultados apuntan a que la colonización natural espontánea es un proceso habitual en terraplenes, aunque su manifestación es sitio-dependiente y está condicionado por factores como la edad y las características del territorio adyacente. Sin embargo, dada la forma en que se abordaba ese estudio (grandes superficies, uso de fotografías aéreas y bases de datos), no era posible ver respuestas diferenciales para distintas especies y diferentes estructuras del paisaje en el entorno de la carretera. Por ello, en el **Capítulo 3** se profundiza en el conocimiento de la colonización de especies leñosas en taludes de carretera con un estudio de campo que permite diferenciar las distintas especies arbóreas . Para ello se han elegido todos los taludes (terraplenes y desmontes) existentes a lo largo de 54 km de la autovía A1 a su paso por las provincias de Segovia y Burgos. A esta escala más detallada los objetivos concretos de este capítulo son describir la diversidad de árboles capaces de colonizar espontáneamente los taludes de carretera, así como analizar la influencia que tienen tanto las características de micrositio como el paisaje que rodea la carretera en este proceso de colonización. Concretamente se trata de responder a las siguientes preguntas: 1) ¿Qué especies de árboles son capaces de colonizar las taludes de las carreteras? 2) ¿Afectan las características del paisaje circundante a la capacidad de colonización de cada especie? 3) ¿Está la llegada de semillas limitada por la existencia de fuentes de semillas en áreas cercanas? 4) El éxito del establecimiento de las diferentes especies de árboles depende de las características físicas de los taludes? Con las respuestas a estas preguntas, y a las plateadas en el Capítulo 2 se trata de afrontar el primer objetivo general de la tesis, analizando la idoneidad de la sucesión natural y la restauración pasiva como un mecanismo adecuado

para restaurar ecosistemas nóveles o degradados y, en particular, para la restauración de la vegetación leñosa en taludes de carreteras. En ambos capítulos se resalta la gran importancia que tiene el entorno próximo a la carretera en el proceso de colonización, lo que parece indicar la existencia de flujos efectivos entre los taludes de carretera y el territorio circundante.

En el **Capítulo 4** se profundiza en las consecuencias de estas conexiones entre taludes y entornos cercanos, analizado la composición y estructura de la comunidad de plantas perennes en los márgenes de una carretera. El estudio se realiza en la autovía A3 en el límite entre las provincias de Madrid y Cuenca, que atraviesa un paisaje fragmentado y de alto valor para la conservación, comparando la vegetación de los remanentes de hábitat de una zona agrícola y de una zona no fragmentada con la existente en distintos tipos de márgenes de la carretera (terraplenes, desmontes y cunetas). Esta comparación se realiza tanto a nivel de especies como de comunidades. Además, se analiza si las diferencias entre las especies y comunidades encontradas en los márgenes de las carreteras son dependientes de las diferentes características constructivas de cada tipo de margen. Específicamente se trata de responder a la siguiente pregunta: ¿Que relación hay entre las comunidades de plantas perennes de los márgenes de la carretera y las comunidades en zonas de remanentes de hábitats a nivel paisaje? Con este conocimiento se busca comprender si una adecuada gestión en los márgenes de las carreteras pueden promover su capacidad para generar o mejorar ciertos servicios ecosistémicos debilitados, concretamente los relacionados en la creación de refugios para especies y comunidades de plantas de interés, con las implicaciones para la conservación de la biodiversidad que ello conlleva.

Los resultados del Capítulo 4 destacan cómo la mayoría de las especies presentes en los remanentes de vegetación natural están presentes también en los márgenes de la carretera, aunque configurando comunidades diferentes. El papel de reservorio de diversidad

que puede ser asignado a los márgenes de carretera parece indicar fuertes interconexiones entre distintos elementos de un paisaje fragmentado. Por ello, en el **capítulo 5** se evalúan los efectos que un conjunto amplio de predictores relacionados tanto con las características del suelo como con factores que actúan a escala de paisaje (conectividad y área entre fragmentos, así como los posibles efectos de la distancia a una autovía) tienen sobre la comunidad de plantas perennes en remanentes de vegetación natural. A su vez, la comunidad de plantas perennes se ha caracterizado también con un conjunto amplio de variables descriptivas relacionadas con grupos funcionales de plantas, con parámetros de diversidad taxonómica o con la composición florística de la propia comunidad. Este estudio se realiza en la misma región y con los mismos fragmentos analizados en el capítulo 4. Específicamente, las preguntas a responder en este capítulo son: 1) ¿Todos los predictores considerados en nuestro estudio son responsables de la configuración de las comunidades de plantas de los remanentes? 2) ¿Que características de la comunidad (grupos funcionales, diversidad taxonómica o composición florística) sintetiza mejor la respuesta de la comunidad de plantas en su conjunto? 3) ¿La distancia a la carretera tiene algún efecto en la composición y estructura de la comunidad de plantas de los remanentes? Respondiendo a estas preguntas buscamos aumentar el conocimiento necesario para mejorar la conservación y restauración de las comunidades de yesos en ambientes fragmentados, así como conocer el papel que juegan las carreteras en la canalización de flujos en dichos ambientes y las implicaciones que ello tendría para gestores e investigadores.

BIBIOGRAFÍA

Aschmann, H. 1973. Distribution and Peculiarity of Mediterranean Ecosystems. In *Mediterranean type ecosystems*, pp. 11–19.

Balaguer, L., Valladares, F., & Mola, I. 2011. Restauración ecológica e infraestructuras de transporte: definiciones, problemas y desafíos. In Valladares, F., Balaguer, L., Mola, I., Escudero, A.,

& Alfaya, V. (eds.), *Restauración ecológica de áreas afectadas por infraestructuras de transporte. Bases científicas para soluciones técnicas*, Fundacion Biodiversidad, Madrid, España.

Benton, T.G., Vickery, J.A., & Wilson, J.D. 2003. Farmland biodiversity: Is habitat heterogeneity the key? *Trends in Ecology and Evolution* 18: 182–188.

Bochet, E., & García-Fayos, P. 2004. Factors controlling vegetation establishment and water erosion on motorway zlopes in Valencia, Spain. *Restoration Ecology* 12: 166–174.

Bochet, E., García-Fayos, P., & Tormo, J. 2007. Road slope revegetation in semiarid Mediterranean environments. Part I: seed dispersal and spontaneous colonization. *Restoration Ecology* 15: 88–96.

Bohrer, G., Katul, G.G., Nathan, R., Walko, R.L., & Avissar, R. 2008. Effects of canopy heterogeneity, seed abscission and inertia on wind-driven dispersal kernels of tree seeds. *Journal of Ecology* 96: 569–580.

Bonet, A. 2004. Secondary succession of semi-arid Mediterranean old-fields in south-eastern Spain: Insights for conservation and restoration of degraded lands. *Journal of Arid Environments* 56: 213–233.

Bruno, J.F., Stachowicz, J.J., & Bertness, M.D. 2003. Inclusion of facilitation into ecological theory. *Trends in Ecology and Evolution* 18: 119–125.

Bruun, H.H. 2000. Patterns of species richness in dry grassland patches in an agricultural landscape. *Ecography* 23: 641–650.

Cano, A., Navia, R., Amezaga, I., & Montalvo, J. 2002. Local topoclimate effect on short-term cutslope reclamation success. *Ecological Engineering* 18: 489–498.

Coffin, A.W. 2007. From roadkill to road ecology: A review of the ecological effects of roads. *Journal of Transport Geography* 15: 396–406.

Cuperus, R., Canters, K.J., & Piepers, A.A.G. 1996. Ecological compensation of the impacts of a road. Preliminary method for the A50 road link (Eindhoven-Oss, The Netherlands). *Ecological Engineering* 7: 327–349.

Debinski, D.M., & Holt, R.D. 2000. A survey and overview of habitat fragmentation experiments. *Conservation Biology* 14: 342–355.

Dickie, J.B., Gajjar, K.H., Birch, P., & Harris, J.A. 1988. The survival of viable seeds in stored topsoil from opencast coal workings and its implications for site restoration. *Biological Conservation* 43: 257–265.

Fahrig, L. 2013. Rethinking patch size and isolation effects: The habitat amount hypothesis. *Journal of Biogeography* 40: 1649–1663.

Forman, R.T.T. 2000. Estimate of the Area Affected Ecologically by the Road System in the United States. *Conservation Biology* 14: 31–35.

Forman, R.T.T., & Alexander, L.E. 1998. Road and their major ecological effects. *Annual Review of Ecology and Systematics* 29: 207–231.

Fu, W., Liu, S., Degloria, S.D., Dong, S., & Beazley, R. 2010. Characterizing the "fragmentation–barrier" effect of road networks on landscape connectivity: A case study in Xishuangbanna, Southwest China. *Landscape and Urban Planning* 95: 122–129.

García-Palacios, P., Bowker, M.A., Maestre, F.T., Soliveres, S., Valladares, F., Papadopoulos, J., & Escudero, A. 2011. Ecosystem development in roadside grasslands: biotic control, plant-soil interactions, and dispersal limitations. *Ecological applications* 21: 2806–21.

García-Palacios, P., Soliveres, S., Maestre, F.T., Escudero, A., Castillo-Monroy, A.P., & Valladares, F. 2010. Dominant plant species modulate responses to hydroseeding, irrigation and fertilization during the restoration of semiarid motorway slopes. *Ecological Engineering* 36: 1290–1298.

García, D., Zamora, R., & Amico, G.C. 2010. Birds as suppliers of seed dispersal in temperate ecosystems: conservation guidelines from real-world landscapes. *Conservation Biology* 24: 1070–1079.

Gelbard, J.L., & Belnap, J. 2003. Roads as conduits for exotic plant invasions in a semiarid landscape. *Conservation Biology* 17: 420–432.

Gómez-Aparicio, L., Zamora, R., Gómez, J.M., Hódar, J.A., Castro, J., & Baraza, E. 2004. Applying plant facilitation to forest restoration: a meta-analysis of the use of shrubs as nurse plants. *Ecological Applications* 14: 1128–1138.

Harrison, S. 1999. Local and regional diversity in a patchy landscape: Native, alien, and endemic herbs on serpentine. *Ecology* 80: 70–80.

Hartley, M. 2002. Rationale and methods for conserving biodiversity in plantation forests. *Forest Ecology and Management* 155: 81–95.

Hodačová, D., & Prach, K. 2003. Spoil heaps from brown coal mining: technical reclamation versus spontaneous revegetation. *Restoration Ecology* 11: 385–391.

Holl, K. 2002. Long-term vegetation recovery on reclaimed coal surface mines in the eastern USA. *Journal of Applied Ecology* 39: 960–970.

Hooke, R., Martín-Duque, J., & Pedraza, J. 2012. Land transformation by humans: A review. *GSA Today* 22: 4–10.

Jarvis, S., Fielder, H., Hopkins, J., Maxted, N., & Smart, S. 2015. Distribution of crop wild relatives of conservation priority in the UK landscape. *Biological Conservation* 191: 444–451.

Jim, C.Y. 1998. Physical and chemical properties of a Hong Kong roadside soil in relation to urban tree growth. *Urban Ecosystems* 2: 171–181.

Jiménez, M.D., Ruíz Capillas, P., Mola, I., Pérez-Corona, E., Casado, M.A., & Balaguer, L. 2011. Soil development at the roadside: a case study of a novel ecosystem. *Land Degradation & Development & Development* 24: 564–574.

Jones, C., Lawton, J., & Shachak, M. 1994. Organisms as ecosystem engineers. *Ecosystem Management* 69: 373–386.

21

Jordano, P., & Godoy, J. 2002. The dynamics of frugivore- generated seed shadows: demographic and genetic effects. In Levey, D.J., Silva, W., & Galetti, M. (eds.), *Seed dispersal and frugivory: ecological, evolutionary, and conservation*, pp. 305–321. CABI Publishing, Wallingford.

Karp, D.S., Rominger, A.J., Zook, J., Ranganathan, J., Ehrlich, P.R., & Daily, G.C. 2012. Intensive agriculture erodes ß-diversity at large scales. *Ecology Letters* 15: 963–970.

Kovář, P. 2004. Natural recovery of human-made deposits in landscape (biotic interactions and ore/ash-slag artificial ecosystems). *Academia, Prague*

de la Riva, E.G., Casado, M.A., Jiménez, M.D., Mola, I., Costa-Tenorio, M., & Balaguer, L. 2011. Rates of local colonization and extinction reveal different plant community assembly mechanisms on road verges in central Spain. *Journal of Vegetation Science.* 22: 292–302.

Lugo, A.E., & Gucinski, H. 2000. Function, effects, and management of forest roads. *Forest Ecology and Management* 133: 249–262.

Luzuriaga, A.L., Sánchez, A.M., Maestre, F.T., & Escudero, A. 2012. Assemblage of a semi-arid annual plant community: abiotic and biotic filters act hierarchically. *PloS One* 7: e41270.

Maheu-Giroux, M., & Blois, S. 2006. Landscape ecology of Phragmites australis invasion in networks of linear wetlands. *Landscape Ecology* 22: 285–301.

Méndez, M., García, D., Maestre, F.T., & Escudero, A. 2008. More Ecology is Needed to Restore Mediterranean Ecosystems: A Reply to Valladares and Gianoli. *Restoration Ecology* 16: 210–216.

Mola, I., Jiménez, M.D., López-Jiménez, N., Casado, M.A., & Balaguer, L. 2011. Roadside Reclamation Outside the Revegetation Season: Management Options under Schedule Pressure. *Restoration Ecology* 19: 83–92.

Moreno, J.C. 2008. *Lista Roja de la Flora Vascular Española*. Dirección General de Medio Natural y Política Forestal Ministerio de Medio Ambiente y Medio rural y Marino Y Sociedad Española de Biología de la Conservación de Plantas, Madrid, España.

Münzbergová, Z. 2004. Effect of spatial scale on factors limiting species distributions in dry grassland fragments. *Journal of Ecology* 92: 854–867.

Münzbergová, Z., & Herben, T. 2005. Seed, dispersal, microsite, habitat and recruitment limitation: identification of terms and concepts in studies of limitations. *Oecologia* 145: 1–8.

Nathan, R., Horn, H.S., Chave, J., & Levin, S.A. 2002. Mechanistic models for tree seed dispersal by wind in dense forests and open landscapes. In Levey, D.J., Silva, W.R., & Galetti, M. (eds.), *Seed dispersal and frugivory: Ecology, Evolution and Conservation*, pp. 69–82. CABI Publishing, Wallingford, Oxon, UK.

Noordijk, J., Schaffers, A.P., Heijerman, T., & Sýkora, K. V. 2011. Using movement and habitat corridors to improve the connectivity for heathland carabid beetles. *Journal for Nature Conservation* 19: 276–284.

Novák, J., & Prach, K. 2003. Vegetation succession in basalt quarries: Pattern on a landscape scale. *Applied Vegetation Science* 6: 111–116.

Parker, V.T. 1997. The Scale of Successional Models and Restoration Objectives. *Restoration Ecology* 5: 301–306.

Perelman, S.B., Burkart, S.E., & León, R.J.C. 2003. The role of a native tussock grass (Paspalum quadrifarium Lam.) in structuring plant communities in the Flooding Pampa grasslands, Argentina. *Methods* 12: 225–238.

Pounden, E., Greene, D.F., Quesada, M., & Contreras Sánchez, J.M. 2008. The effect of collisions with vegetation elements on the dispersal of winged and plumed seeds. *Journal of Ecology* 96: 591–598.

Prach, K., & Hobbs, R. 2008. Spontaneous succession versus technical reclamation in the restoration of disturbed sites. *Restoration Ecology* 16: 363–366.

Prach, K., Pysek, P., & Jarosík, V. 2007. Climate and pH as determinants of vegetation succession in Central European man-made habitats. *Journal of Vegetation Science* 18: 701–710.

Pueyo, Y., & Alados, C.L. 2007. Effects of fragmentation, abiotic factors and land use on vegetation recovery in a semi-arid Mediterranean area. *Basic and Applied Ecology* 8: 158–170.

Pueyo, Y., Alados, C.L., Barrantes, O., Komac, B., & Rietkerk, M. 2008. Differences in gypsum plant communities associated with habitat fragmentation and livestock grazing. *Ecological Applications* 18: 954–964.

Rey Benayas, J.R., Bullock, J.M., & Newton, A.C. 2008. Creating woodland islets to reconcile ecological restoration, conservation, and agricultural land use. *Frontiers in Ecology and the Environment* 6: 329–336.

Rösch, V., Tscharntke, T., Scherber, C., & Batáry, P. 2013. Landscape composition, connectivity and fragment size drive effects of grassland fragmentation on insect communities. *Journal of Applied Ecology* 50: 387–394.

Saunders, D.A., Hobbs, R.J., & Margules, C.R. 1991. Biological Consequences of Ecosystem Fragmentation: A Review. *Conservation Biology* 5: 18–32.

Schurr, F., Steinitz, O., & Nathan, R. 2008. Plant fecundity and seed dispersal in spatially heterogeneous environments: models, mechanisms and estimation. *Journal of Ecology* 96: 628–641.

Spooner, P., & Smallbone, L. 2009. Effects of road age on the structure of roadside vegetation in South-eastern Australia. *Agriculture, Ecosystems & Environment* 129: 57–64.

Tikka, P., Högmander, H., & Koski, P. 2001. Road and railway verges serve as dispersal corridors for grassland plants. *Landscape ecology* 16: 659–666.

Tikka, P., Koski, P., Kivelä, R., & Kuitunen, M. 2000. Can grassland plant communities be preserved on road and railway verges? *Applied Vegetation Science* 3: 25–32.

Tormo, J., Bochet, E., & García-fayos, P. 2006. Is seed availability enough to ensure colonization success?An experimental study in road embankments. *Ecological Engineering* 26: 224–230.

Tormo, J., García-Fayos, P., & Bochet, E. 2008. Relative importance of plant traits and ecological filters in road embankment revegetation under semiarid Mediterranean conditions. *Ecological Engineering* 33: 258–264.

de Torre, R. 2014. Procesos ecologicos en el emsamblaje de comunidades en taludes de carretera y su aplicacion en la restauracion ecologica. Universidad de Alcalá de Henares

de Torre, R., Jiménez, M.D., Ramírez, Á., Mola, I., Casado, M.A., & Balaguer, L. 2015. Use of restoration plantings to enchance bird seed dispersal at the roadside: failures and prospects. *Journal of Environmental Engineering and Landscape Management* 23: 302–311.

Trombulak, S.C., & Frissell, C.A. 2000. Review of ecological effects of roads on terrestrial and aquatic communities. *Conservation Biology* 14: 18–30.

Turner, I. 1996. Species Loss in Fragments of Tropical Rain Forest: A Review of the Evidence. *The Journal of Applied Ecology* 33: 200–209.

Verdú, M., & García-Fayos, P. 1996. Nucleation processes in a mediterranean bird-dispersed plant. *Functional Ecology* 10: 275–280.

Vitousek, P.M., Mooney, H. a, Lubchenco, J., & Melillo, J.M. 1997. Human Domination of Earth᾽ s Ecosystems. *Science* 277: 494–499.

Wilby, A., & Shachak, M. 2004. Shrubs, granivores and annual plant community stability in an arid ecosystem. *Oikos* 106: 209–216.

Wynhoff, I., Gestel, R., Swaay, C., & Langevelde, F. 2010. Not only the butterflies: managing ants on road verges to benefit Phengaris (Maculinea) butterflies. *Journal of Insect Conservation* 15: 189–206.

Capítulo 2
Woody colonization of road embankments: A large spatial scale survey in central Spain

J.M. Arenas, A. Escudero, S. Magro, L. Balaguer, M. A. Casado

Research Paper

Woody colonization of road embankments: A large spatial scale survey in central Spain

Juan M. Arenas [a,*], Adrián Escudero [b], Sandra Magro [a], Luis Balaguer [c], Miguel A. Casado [a]

[a] Departamento de Ecología, Universidad Complutense de Madrid, 28040 Madrid, Spain
[b] Departamento de Biología and Geología, Universidad Rey Juan Carlos, Móstoles 28933, Spain
[c] Departamento de Biología Vegetal I, Universidad Complutense de Madrid, 28040 Madrid, Spain

HIGHLIGHTS

- Woody colonization on embankments shows a highly site-dependent pattern.
- Spontaneous succession may be an effective passive restoration tool on embankments.
- Conservation measures on the surrounding matrix are critical for roadside restoration.

ARTICLE INFO

ABSTRACT

Planting of woody species is a commonly used method to restore road embankments. Given the importance of road verges as potential corridors and refuge for biodiversity, natural plant regeneration processes may also play an important role in establishing vegetation into these novel landscape elements. Most studies on woody colonization of roadsides have considered only a few sites covering a very limited environmental range. Therefore, it is unclear whether or not there are general patterns that may explain the development of woody vegetation. We analyzed woody vegetation colonization in embankments over a large and heterogeneous territory, using aerial photographs, available repositories of environmental and land management data sets and some embankment features. We addressed the following questions: (1) To what extent does the presence of planted woody plants influence patterns of natural recruitment in road embankments? and (2) What are the key factors underlying natural/passive plant colonization in road embankments? We used Multi-Model Inference (MMI) analysis to model woody vegetation cover. According to our results, woody-planted vegetation does not have a facilitating effect on natural colonization, questioning the efficiency of reforestation measures in the ecological integration of areas affected by road construction. Passive natural plant colonization occurs spontaneously in road verges and shows a highly site-dependent pattern, driven mainly by the age of embankments and the immediate surrounding vegetation. Therefore, we suggest that natural succession may be sufficiently effective as a passive restoration measure on embankments in the long term.

© 2015 Elsevier B.V. All rights reserved.

1. Introduction

Road verges act as a source/sink for biodiversity, and represent important connectors between habitat remnants, by providing continuous habitat linkages that aid in the dispersal of both native and exotic flora (Coulson, Spooner, Lunt, & Watson, 2013; Jodoin et al., 2008; Tikka, Högmander, & Koski, 2001; Zeng et al., 2011). At a landscape scale, they increase environmental heterogeneity and can provide refugia for restricted-range and other native species (Spooner & Smallbone, 2009; Tikka, Koski, Kivelä, & Kuitunen, 2000). This function is critical in fragmented landscapes where linear marginal lands can often harbour plant species from the surrounding areas (Corbit, Marks, & Gardescu, 1999; Schmitz, Sánchez, & de Aranzabal, 2007).

Road embankments and other areas immediately adjacent to road surfaces are newly created structures susceptible to colonization and succession (Bochet, García-Fayos, & Tormo, 2007; Jiménez et al., 2013). These areas affected by road construction (known as

* Corresponding author at: Departamento de Ecología, Facultad de Ciencias Biológicas, Universidad Complutense de Madrid, C/José Antonio Novais, 2, 28004 Madrid, Spain. Tel.: +34 913945123.

E-mail addresses: jmarenas@ucm.es (J.M. Arenas), adrian.Escudero@Urjc.Es (A. Escudero), s.Magro@Pdi.Ucm.Es (S. Magro), balaguer@Bio.Ucm.Es (L. Balaguer), mcasado@Ucm.Es (M.A. Casado).

the "road effect zone"; Forman et al., 2003) can also play a key role in plant community dynamics by generating new ecological flows inwards and outwards from the road verge (Lugo & Gucinski, 2000). However, after construction, road embankments are often devoid of all vestiges of biological communities, where hydrological and geomorphological features have been greatly altered. Thus, some restoration measures are commonly applied to increase ecosystem carrying capacity.

Under Mediterranean conditions, current roadside restoration measures include topsoil spreading, hydroseeding with commercial seeds of fast-growing plant species, and in some cases, low density plantings of tree seedlings and shrubs. Although these plantings are typically performed for aesthetic purposes, this vegetation is meant to play an important role on soil stabilization and have a catalytic effect on the succession process (Singh, Raghubanshi, & Singh, 2002). Woody vegetation is a well-known landscape engineer (Jones, Lawton, & Shachak, 1994; Wilby & Shachak, 2004) acting as a facilitator for the establishment of other species by improving abiotic conditions, such as enhanced soil nutrients and water availability and microclimatic heterogeneity (Bruno, Stachowicz, & Bertness, 2003; Gómez-Aparicio et al., 2004). Moreover, woody vegetation nuclei are expected to provide local seed sources and serve as attractors of seed-dispersal vectors, increasing connectivity between different patches at the landscape scale (Rey Benayas, Bullock, & Newton, 2008). In many cases, woody species introduced in roadsides areas are often not well-adapted to the local environment that results from the interaction of Mediterranean climatic conditions and the stressful conditions derived from construction processes (Hartley, 2002). In this sense, there is great uncertainty associated with the performance of plantings in these environments, which translates into higher costs for the companies responsible for roadside maintenance and conservation.

Many studies, however, highlight the importance of promoting natural colonization from surrounding vegetation as a useful restoration measure, which is highly cost effective and also has the advantage of increasing local diversity in these human-made ecosystems (Prach & Hobbs, 2008). Spontaneous plant colonization in roadsides has been positively correlated with surrounding vegetation structure and the availability of seed sources (Bochet, García-Fayos, & Tormo, 2007). In some cases, construction and maintenance of the road (i.e., earthworks, grading) may favour the arrival of woody plants adapted to frequent disturbances (Spooner, 2005; Spooner, Lunt, Briggs, & Freudenberger, 2004). However, the steepness of the slope, the aspect and the area of the road-slopes mainly constrain the arrival and establishment of long-term viable plant communities (Cano, Navia, Amezaga, & Montalvo, 2002; Deckers, Becker, De Honnay, Hermy, & Muys, 2005). Furthermore, the age of the roadslope, described as the time elapsed since the road was constructed (García-Palacios et al., 2011), seems to be a relevant driver of plant community development (i.e., changes in plant cover and composition) in these scenarios (Olander, Scatena, & Silver, 1998; Spooner & Smallbone, 2009). However, most studies of natural succession in road verges have considered only a few sites covering a very limited geographical area (but see Deckers et al., 2005; Spooner & Smallbone, 2009). Thus, it is difficult to determine whether the results obtained reflect a general pattern or are site-dependent. Moreover, the effect of other environmental factors operating at larger scales such as land use, lithology or climate, have not been previously explored in these environments. The effects of both regional and local factors and corresponding patterns can only be assessed by considering many sampling points distributed over a vast territory (Lugo & Gucinski, 2000; Novák & Prach, 2003; Prach, Pysek, & Jarosík, 2007).

During the last few decades, great effort has been devoted to build up a restoration ecology paradigm (Choi, 2007). However, its complete scope and universality is constrained by the lack of

studies conducted across large temporal and spatial scales (Manning, Lindenmayer, & Fischer, 2006; Novák & Prach, 2003; Parker, 1997). Recognizing general patterns and processes involved in the colonization of road verges is highly demanding in so far as regeneration of native woody species can be considered a surrogate of restoration success (Prach & Hobbs, 2008). Moreover, understanding the factors affecting roadside vegetation dynamics at larger scales would shed light on the ecosystem services derived by these habitats (e.g., biological corridors and refuge of biodiversity) and lead to restoration measures. With this in mind, the aim of this study was to investigate patterns of woody vegetation establishment in road verges over a large and environmentally heterogeneous territory. Our working hypothesis is that landscape configuration and seed source patterns are critical (even more than tree-plantings) in the spontaneous recovery of woody vegetation in road verges. Specifically, we addressed the following questions: (a) To what extent does the presence of planted woody plants influence patterns of natural recruitment in road verges? and (b) What are the key factors (site, large scale) that influence the recruitment of woody plants in road verges? We modelled the performance of woody vegetation by Multi-Model Inference (MMI) and a complete set of predictors taken across local and regional scales (aerial photographs, available repositories of environmental and land management data sets and local features).

2. Materials and methods

2.1. Study area

We conducted the study on the motorway and highway network in the region of Madrid, Spain, covering an area of 8022 km². This network has an approximate length of 800 km, spanning an altitudinal range from 430 m a.s.l. at the Tajo River Valley, to 1430 m a.s.l. at the Guadarrama Sierra. The climate is mostly continental Mediterranean with mesoclimatic variations associated with altitude. The mean annual temperature along the road network varies between 8.9 °C and 14.5 °C and mean annual rainfall ranges from 389 to 822 mm (Ninyerola, Pons, & Roure, 2005). This large territory covers two major lithographic and geographic areas: a mountain area and its ramp, formed by acid rocks (granites, gneisses and arkoses); and moors and countryside areas, mainly dominated by basic materials (limestone, gypsum and marls). Approximately two-thirds of the studied road network has been constructed on a basic substrate. Climate, topography and human activities have contributed to landscape heterogeneity by introducing a wide variety of vegetation types: forests (e.g., Scots pines, holm oaks, Pyrenean oaks), scrublands, grasslands and crops.

2.2. Site inventory

Among the different components of road verges, we focused on embankments because they provide a more favourable testing ground for colonization processes as they are isolated patches, spatially well-defined and devoid of vegetation after construction. We identified and characterized the embankments with aerial photographs taken in 2009 by the Aerial Orthophotography National Plan of the National Geographic Institute of Spain (2011). We preselected all road embankments with at least a 6 m width. From this first set of sites, we discarded poorly defined roadfills as well as metropolitan embankments. Ultimately, we retained 351 sites (Fig. 1).

Embankments were polygonized and characterized at different scales by measuring a complete set of variables (Table 1) with ArcGIS 9.3 (ESRI, 2011). The complete list included the geographical coordinates (X and Y centroids), aspect, area and perimeter of the

Fig. 1. Motorway and highway network (grey lines) in the region of Madrid. Black dots indicate embankments considered in this study.

Table 1
Predictors (and their abbreviations) considered in each MMI-model.

Scale	Predictors considered
Local	
Planted woody plant cover on embankments	Planted woody plant cover (PE)
Short-distance surrounding cover (0–20 m)	Natural woody plant cover (N20)
	Planted woody plant cover (P20)
Medium-distance surrounding cover (20–150 m)	Natural woody plant cover (N150)
	Planted woody plant cover (P150)
Embankment features	Area (Area)
	Patton shape Index (PI)
	Age (Age)
	Thermotopographic index (TTG)
Regional	
Climate	Average annual temperature (AAT)
	Annual precipitation (Prec)
Others	Corine Land Cover (CLC)
	Lithology (Lit)
Geographical[a]	Longitude (X)
	Latitude (Y)

[a] Latitude and longitude coordinates were included to control potential effects of spatial autocorrelation between sites (Bini et al., 2009).

embankment. To assess insolation conditions, we calculated the thermotopographic index (TTG) following Gandullo (1997). This index combines latitude, slope and aspect. To calculate the patch shape we combined area and perimeter using the Patton index (PI; Patton, 1975), which varies from 1 to infinite. Greater values of PI indicate an increase in perimeter-to-area ratio, which corresponds to embankments with more edge per unit surface area.

We used the National Geology Map of Spain to assign lithology classified as acid or basic substrate. We obtained average annual temperature and total annual precipitation from Ninyerola et al. (2005), using 'Miramon' GIS software (Pons, 2010). To assess the type of vegetation in the surrounding landscape we used the Corine Land Cover map (European Environment Agency, 2007). We merged Corine categories into 3 types: periurban, intensive

agricultural and forestry (including agroforestry lands, scrublands and grasslands). To estimate the age of each embankment (time elapsed since embankment construction), we surveyed all the constructive projects in the territory provided by the Department for the Maintenance of Spanish National Roads. Finally, to cross-check constructive projects data and to complete other missing information, we examined the temporal sequence of orthophotos (1956, 1975, 1991, 1999, 2001, 2006, 2008 and 2009) provided by the Institute of Statistics of the Community of Madrid (2012).

2.3. Vegetation sampling

We estimated plant cover in each embankment by measuring the percentage of woody vegetation in the 2009 orthophotos. Pixel resolution (0.5 m) allowed us to discriminate medium to large plant sizes (>3 m^2 of canopy area). Considering the spatial pattern of the woody vegetation and the pattern of individual plant sizes, woody plant cover was classified as natural colonization (sparse with different sized individuals) or planted (regular patterns with homogeneously sized individuals). We catalogued each isolated woody individual or homogeneous patch detected in an embankment within any of these categories and calculated the total cover of each category. Finally, we measured the influence of surrounding matrices on the plant colonization processes by assessing the percentage of surrounding woody vegetation (both natural and planted) at two distances from the edge of each embankment: short-distance (0–20 m) and medium-distance (20–150 m). It has been demonstrated that most species found in embankments originate from surrounding vegetation within 150 m (Bochet, García-Fayos, & Tormo, 2007).

2.4. Data analyses

We used Multi-Model Inference techniques (MMI; Burnham & Anderson, 2002) to determine the drivers of colonization and establishment of woody vegetation in road embankments. MMI has been increasingly used and recommended when dealing with observational data collected over large spatial scales and environmental gradients (Johnson & Omland, 2004; Maestre et al., 2012). Unlike the classical approach to fitting models based on selection of the best model followed by traditional hypothesis testing, MMI uses information theory to rank all the predictor variables according to their relative importance. Specifically, we modelled the natural woody cover on embankments (NE, response variable) by considering a wide range of predictors associated with each embankment (Table 1). To elucidate the relative contribution of predicting variables to the observed pattern, we generated all possible models by combining all predictors (2^n models with n predictors variables; $n = 15$). All these models were ranked according to Akaike Information Criterion (AIC). The AIC was then transformed into ΔAIC, which is the difference between the AIC of each model and the minimum AIC obtained for all models. Finally, the Akaike weight of each model (w_i) was calculated by using Eq. (1). We then obtained the relative weight of each predictor (w_x) following Eq. (2).

$$W_i = \frac{\exp((-\Delta AICi)/2)}{\sum_r^1 \exp((-\Delta AICr)/2)} \quad \text{Burnham and Anderson (2002)} \quad (1)$$

$$W_x = \sum_1^n W_{in} \quad \text{Burnham and Anderson (2002)} \quad (2)$$

w_x ranges between 0 and 1 and values closer to 1 correspond to the most important variables. Because the MMI techniques only detect the relative importance of each predictor, the direction and magnitude of its effect was determined by the model-averaged parameter estimate, which is calculated using the average of the coefficient

estimates from each model, weighted by its Akaike weight (w_i) (Burnham & Anderson, 2002). The variance explained by the best model according to AIC was used as a surrogate for the explained variance for MMI model. All analyses were performed with R (R Development Core Team, 2012) with the additional packages "car" (Fox & Weisberg, 2011) and "glmulti" (Calcagno, 2012).

3. Results

The age of construction of road embankments ranged between 0 and 37 years with an irregular distribution corresponding to different road construction/modification events (Fig. 2a). Their sizes were also highly variable, ranging between 175 and 37,397 m^2. Among the sampled embankments, 47% were distributed in intensive agricultural areas, and 38% in forestry-dominated landscapes. Natural woody plant cover was generally low but highly variable among embankments with an average of 4.7% that ranged from 0 to 85%, and an average of planted woody cover of 2.0% varying between 0 and 90%. The mean percentage of surrounding natural woody vegetation at short distances (0–20 m) was 5.3%, with few sites reaching values greater than 30% (Fig. 2b).

The variance explained by the best model for the natural woody cover on embankments was 43.8%. The age of the embankment was one of the most important predictors for this MMI model (Fig. 3), with the oldest embankments being those with the highest woody cover (Table 2). Natural woody plant cover in the immediate surroundings (N20) was also an important predictor (Fig. 3). By contrast, natural woody cover at medium distances (N150) had weak explanatory effects, although this variable was strongly correlated with its short-distance counterpart ($r = 0.747$). Planted woody vegetation did not have an important effect on the colonization of embankments by natural vegetation (Fig. 3: w_x values of 0.59, 0.59 and 0.32, for woody plant cover on embankments, immediate surrounding and medium distances, respectively). Other local predictors considered such as TTG, embankment area and Patton shape index, had a relatively high weight ($w_x = 0.79$, 0.72, 0.70, respectively). According to the model-averaged parameter estimate for each of these predictors (Table 2), road embankments with less sun exposure, higher area and a lower perimeter-to-area ratio showed the highest natural woody vegetation cover. Finally, abiotic regional predictors, such as annual precipitation, average annual temperature and lithology along with land uses were of less importance (Fig. 3).

4. Discussion

Our findings show the existence of a clear pattern of colonization by natural woody vegetation in road embankments under
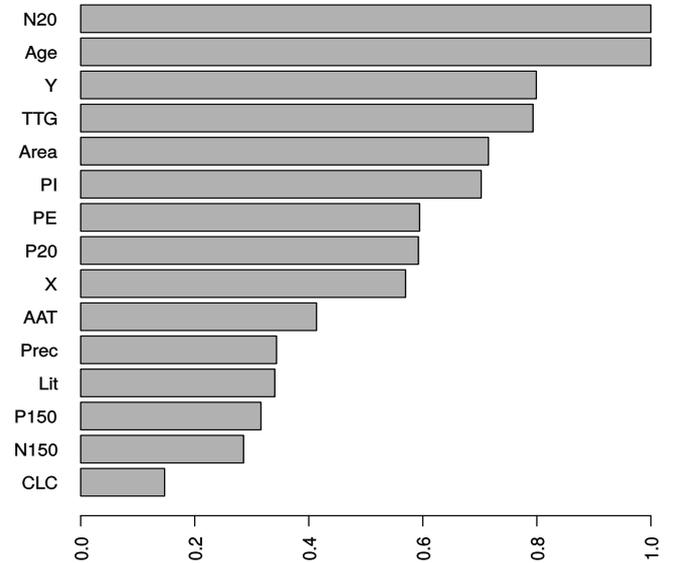
Fig. 3. Relative importance (w_x) of the predictors for modelled variables in the MMI model for natural woody plant cover (NE). Abbreviations are indicated in Table 1.

a wide array of climate, geology and land use scenarios in the central Spain region. Although the characteristics of the study area may have influenced these results, the type of relationships found (i.e., prevalence of local factors) suggest they are potentially transferable to other territories. Any increase in natural woody plants cover was mainly influenced by local conditions such as age since road construction and some surrounding vegetation features. On the contrary, we did not observe an important effect of the planted woody vegetation on embankments, which suggests that the dynamics of planted trees are disconnected from the general dynamics of roadside vegetation. These results question the efficiency of reforestation measures in the restoration and ecological integration of areas affected by road construction, as well as the role of plantings in ecosystem functioning across scales (Balaguer, Escudero, Martín-Duque, Mola, & Aronson, 2014).

Natural woody colonization in road embankments was mainly driven by both age of the embankment and the natural woody cover in the immediate surroundings, which are clearly linked to succession and not necessarily to restoration measures. The increase of woody cover with time is a well-known process on road-slopes after their construction (see Olander et al., 1998; Spooner & Smallbone, 2009). Woody plant colonization can be explained by the simultaneous effect of site conditions (i.e., carrying capacity)
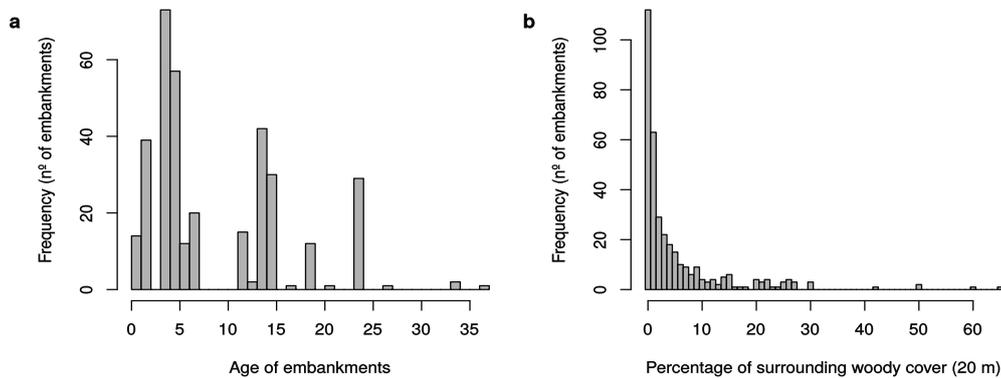
Fig. 2. Distribution of the studied embankments according to age since their construction (a) and their 0–20 m surrounding natural woody cover (b).

Table 2
Model-averaged parameter estimates for each predictor for the natural woody plant cover on the embankments MMI model.

	Coefficient
Planted woody plant cover on embankments	
Planted woody plant cover (PE)	−0.05
Short-distance surrounding cover (0–20 m)	
Natural woody plant cover (N20)	0.51
Planted woody plant cover (P20)	0.126
Medium-distance surrounding cover (20–150 m)	
Natural woody plant cover (N150)	−0.006
Planted woody plant cover (P150)	0.008
Embankment features	
Area (Area)	0.0001
Patton index (PI)	−0.848
Age (Age)	0.376
Climate	
Thermotopographic parameter (TTG)	−1.341
Annual precipitation (Prec)	4.7E−05
Average annual temperature (AAT)	−0.035
Others	
Corine Land Cover (CLC): Agricola	−0.023
Corine Land Cover (CLC): Forestry	0.082
Lithology (Lit): Basic	0.458
Geographical	
Longitude (X)	2.6E−05
Latitude (Y)	−4.6E−05

and dispersal processes (i.e., arrival of propagules) (Münzbergová & Herben, 2005). A general pattern in disturbed sites such as road-slopes is that carrying capacity tends to increase with time. This pattern is a consequence of the establishment of pioneer species, which profoundly influence the soil organic matter inputs in the early stages of ecosystem development facilitating the establishment of new individuals (García-Palacios et al., 2011; Jiménez et al., 2013). Alternatively, this pattern results from an increase in the environmental heterogeneity derived from the existence of gravitational movements of sediments, nutrients and water, which in turn create erosion and accumulation zones along embankments (Jiménez et al., 2013; Magro et al., 2014; Walker, Velázquez, & Shiels, 2009).

It has also been described that the probability of the arrival of propagules increases over time (Jacquemyn, Butaye, Dumortier, Hermy, & Lust, 2001). This probability is dependent on both dispersal efficiency of each individual species and the nature and quality of the surrounding matrix (Jacquemyn et al., 2001). The vegetation from nearby natural remnants acts as a source of propagules (Bochet, García-Fayos, & Tormo, 2007; Coulson et al., 2013; Mola, Jiménez, López-Jiménez, Casado, & Balaguer, 2011) influencing dispersal processes by changes in wind flow (Nathan, Horn, Chave, & Levin, 2002) and movement of seed dispersers (Coulson et al., 2013; Pausas, Bonet, Maestre, & Climent, 2006). The positive effects of the surrounding vegetation at short distances is a reflection of the role of these patches as seed sources, which is dependent on the distance, with a maximum at short distances (Nathan & Muller-Landau, 2000), and on the perch effect caused by trees (Coulson et al., 2013; Howe & Miriti, 2004; Pausas et al., 2006).

Our results also highlighted a secondary set of fine local scale predictors, namely TTG, embankment size and shape (PI). Road restoration studies conducted at a local scale under semi-arid Mediterranean conditions emphasize that plant community development is influenced by embankment aspect, which is mainly related to soil water availability but also to other microclimatic conditions and nutrient content (Bochet, García-Fayos, Alborch, & Tormo, 2007; Cano et al., 2002; Mola et al., 2011). Therefore, less sun-exposed embankments are more favourable for plant

establishment in northern latitude Mediterranean environments (Bochet & García-Fayos, 2004). Sun exposure conditions, measured by the TTG parameter, constrain woody colonization not only in semiarid environment but also in a wide range of climatic situations.

Moreover, in fragmented landscapes, woody cover and colonization have been related to the geometry of patches. For instance, Yao, Holt, Rich, and Marshall (1999) showed that woody colonization proceeded faster in larger patches of disturbed areas than in smaller ones. They also found that larger patches trapped more propagules than smaller ones. Recruited propagules begin a positive feedback loop that facilitates in situ seed production and clonal growth. In line with these results, we found that embankment area was positively correlated to greater natural woody cover. Regarding the shape of embankments, it is known that the higher the perimeter-to-area ratio the greater the "edge effect" (Svoray, Mazor, & Bar (Kutiel), 2006), meaning that edge areas have a higher probability of arrival and establishment of species than core areas (Gonzalez et al., 2010). However, in the present study, woody cover was negatively affected by this "edge effect", being the more compact embankments (i.e., with lower perimeter-to-area ratios) more likely to attain a high woody cover. This effect could be due to competitive exclusion between woody plants and grasses as described elsewhere (Davis, Wrage, & Reich, 1998). On borders frequently exposed to high disturbance regimes, herbaceous plants are better competitors than woody plants. Roadside management in the upper-slope zones may impede the establishment of perennial plants while accumulation of water and nutrients at the lower slope zone may favour colonization by fast growing species.

Surprisingly and contrary to what was described by Prach et al. (2007), we did not find a strong effect of the variables measured at a large scale (macroclimate, lithology and land use) in natural woody plant colonization patterns. These variables may indirectly affect woody vegetation in road embankments through their effects on both the species pool and the spatial patterns of surrounding vegetation (Prach et al., 2007), but do not seem to determine the colonization process itself.

5. Conclusions and implications for practice

The present study contributes not only to improve the understanding of natural woody plant colonization processes in road embankments, but also to aid the design and implementation of better integration measures and the efficient recovery of areas affected by road construction. First, we observed that woody planted vegetation on embankments did not accelerate the development of natural woody vegetation. Woody plantings can be successful when they are made with aesthetic or soil-stabilizing purposes in mind (Singh et al., 2002), but we question their effectiveness in facilitating secondary succession in these human-made ecosystems (Badía, Valero, Gracia, Martí, & Molina, 2007; Booth, Gores, Schuman, & Olson, 1999) as they appear to be having the opposite effect.

Second, we found a general pattern for embankment colonization by woody plants, although it is a highly site-dependent process. This pattern is mainly driven by secondary succession dynamics linked to the age of the embankment and to the nature of the immediate surrounding vegetation, but is also influenced by other local factors. Therefore, our results suggest that, when surrounding vegetation is kept in good condition and embankment features are appropriate, natural vegetation dynamics are sufficiently effective as a passive restoration measure on embankments in the long-term (see also García-Palacios et al., 2011). This could imply that conservation measures on the matrix during the construction stage

could be critical for the woody colonization of these public lands, even more than genuine revegetation measures, which may indeed be counterproductive. In addition, passive restoration can support environmental conservation by promoting the maintenance of regional species pools and allowing the development of ecological flows between roadsides and their surroundings. This could also help to minimize the costs of road maintenance by reducing environmental liabilities for the companies and governments that maintain these infrastructures.

However, this passive restoration requires time, as explained by our results, and managing time in restoration projects is challenging due to conflicts between goals for short-term and long-term recovery of highly disturbed sites (Holl, 2002). Thus, efforts should be oriented towards the development of restoration plans that combine goals at different spatial and temporal scales (Parker, 1997). For instance, there is a need to prevent road slope erosion shortly after construction (Andrés & Jorba, 2000; Cerdà, 2007) and to allow natural succession to act in the medium-term to obtain both environmental and economic benefits.

Acknowledgements

References

Andrés, P., & Jorba, M. (2000). Mitigation strategies in some motorway embankments (Catalonia, Spain). *Restoration Ecology*, 8(3), 268–275. http://dx.doi.org/10.1046/j.1526-100x.2000.80038.x

Badía, D., Valero, R., Gracia, A., Martí, C., & Molina, F. (2007). Ten-year growth of woody species planted in reclaimed mined banks with different slopes. *Arid Land Research and Management*, 21(1), 67–79. http://dx.doi.org/10.1080/15324980601094022

Balaguer, L., Escudero, A., Martín-Duque, J. F., Mola, I., & Aronson, J. (2014). The historical reference in restoration ecology: Re-defining a cornerstone concept. *Biological Conservation*, 176, 12–20. http://dx.doi.org/10.1016/j.biocon.2014.05.007

Bini, L. M., Diniz-Filho, J. A. F., Rangel, T. F. L. V. B., Akre, T. S. B., Albaladejo, R. G., Albuquerque, F. S., et al. (2009). Coefficient shifts in geographical ecology: An empirical evaluation of spatial and non-spatial regression. *Ecography*, 32(2), 193–204. http://dx.doi.org/10.1111/j.1600-0587.2009.05717.x

Bochet, E., & García-Fayos, P. (2004). Factors controlling vegetation establishment and water erosion on motorway slopes in Valencia, Spain. *Restoration Ecology*, 12(2), 166–174. http://dx.doi.org/10.1111/j.1061-2971.2004.0325.x

Bochet, E., García-Fayos, P., Alborch, B., & Tormo, J. (2007). Soil water availability effects on seed germination account for species segregation in semiarid road-slopes. *Plant and Soil*, 295(1–2), 179–191. http://dx.doi.org/10.1007/s11104-007-9274-9

Bochet, E., García-Fayos, P., & Tormo, J. (2007). Road slope revegetation in semiarid Mediterranean environments. Part I: Seed dispersal and spontaneous colonization. *Restoration Ecology*, 15(1), 88–96. http://dx.doi.org/10.1111/j.1526-100X.2006.00194.x

Booth, D., Gores, J., Schuman, G., & Olson, R. (1999). Shrub densities on pre 1985 reclaimed mine lands in Wyoming. *Restoration Ecology*, 7(1), 24–32. http://dx.doi.org/10.1046/j.1526-100X.1999.07103.x

Bruno, J. F., Stachowicz, J. J., & Bertness, M. D. (2003). Inclusion of facilitation into ecological theory. *Trends in Ecology and Evolution*, 18(3), 119–125.

Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference. A practical information-theoretical approach*. New York: Springer-Verlag.

Calcagno, V. (2012). *glmulti: Model selection and multimodel inference made easy*. Retrieved from http://cran.r-project.org/package=glmulti

Cano, A., Navia, R., Amezaga, I., & Montalvo, J. (2002). Local topoclimate effect on short-term cutslope reclamation success. *Ecological Engineering*, 18(4), 489–498. http://dx.doi.org/10.1016/S0925-8574(02)00010-1

Cerdà, A. (2007). Soil water erosion on road embankments in eastern Spain. *Science of the Total Environment*, 378(1–2), 151–155. http://dx.doi.org/10.1016/j.scitotenv.2007.01.041

Choi, Y. D. (2007). Restoration ecology to the future: A call for new paradigm. *Restoration Ecology*, 15(2), 351–353. http://dx.doi.org/10.1111/j.1526-100X.2007.00224.x

Corbit, M., Marks, P. L., & Gardescu, S. (1999). Hedgerows as habitat corridors for forest herbs in central New York, USA. *Journal of Ecology*, 87(2), 220–232. http://dx.doi.org/10.1046/j.1365-2745.1999.00339.x

Coulson, C., Spooner, P. G., Lunt, I. D., & Watson, S. J. (2013). From the matrix to roadsides and beyond: The role of isolated paddock trees as dispersal points for invasion. *Diversity and Distributions*, 1–123. http://dx.doi.org/10.1111/ddi.12135

Davis, M. A., Wrage, K. J., & Reich, P. B. (1998). Competition between tree seedlings and herbaceous vegetation: Support for a theory of resource supply and demand. *Journal of Ecology*, 86(4), 652–661. http://dx.doi.org/10.1046/j.1365-2745.1998.00087.x

Deckers, B., Becker, P., De Honnay, O., Hermy, M., & Muys, B. (2005). Sunken roads as habitats for forest plant species in a dynamic agricultural landscape: Effects of age and isolation. *Journal of Biogeography*, 32(1), 99–109. http://dx.doi.org/10.1111/j.1365-2699.2004.01101.x

ESRI. (2011). *ArcGIS for desktop*. Redlands, CA: Environmental Systems Research Institute, Inc.

European Environment Agency. (2007). *Corine Land Cover*. Retrieved from http://www.ign.es/

Forman, R. T. T., Sperling, D., Bissonette, J. A., Clevenger, A. P., Cutshall, C. D., Dale, V. H., et al. (2003). *Road ecology: Science and solutions*. Washington: Island Press.

Fox, J., & Weisberg, S. (2011). *An R companion to applied regression* (2nd ed.). Thousand Oaks, CA: Sage. Retrieved from http://socserv.socsci.mcmaster.ca/jfox/Books/Companion

Gandullo, J. (1997). Implicaciones térmicas de la topografía: Ensayo de un parámetro termotopográfico. *Investigación Agraria. Sistemas y Recursos Forestales*, 6.

García-Palacios, P., Bowker, M., Maestre, A., Soliveres, F. T., Valladares, S., Papadopoulos, F., et al. (2011). Ecosystem development in roadside grasslands: Biotic control, plant–soil interactions, and dispersal limitations. *Ecological Applications*, 21(7), 2806–2821. http://dx.doi.org/10.1890/11-0204.1

Gómez-Aparicio, L., Zamora, R., Gómez, J. M., Hódar, J. A., Castro, J., & Baraza, E. (2004). Applying plant facilitation to forest restoration: A meta-analysis of the use of shrubs as nurse plants. *Ecological Applications*, 14(4), 1128–1138. http://dx.doi.org/10.1890/03-5084

Gonzalez, M., Ladet, S., Deconchat, M., Cabanettes, A., Alard, D., & Balent, G. (2010). Relative contribution of edge and interior zones to patch size effect on species richness: An example for woody plants. *Forest Ecology and Management*, 259(3), 266–274. http://dx.doi.org/10.1016/j.foreco.2009.10.010

Hartley, M. (2002). Rationale and methods for conserving biodiversity in plantation forests. *Forest Ecology and Management*, 155, 81–95.

Holl, K. (2002). Long-term vegetation recovery on reclaimed coal surface mines in the eastern USA. *Journal of Applied Ecology*, 39, 960–970. http://dx.doi.org/10.1046/j.1365-2664.2002.00767.x

Howe, H. F., & Miriti, M. N. (2004). When seed dispersal matters. *BioScience*, 54(7), 651. http://dx.doi.org/10.1641/0006-3568(2004)054[0651:WSDM]2.0.CO;2

Instituto de estadística de la comunidad de Madrid. (2012). *Nomecalles. Nomenclator oficial y callejero*. Retrieved from http://www.madrid.org/nomecalles/

Jacquemyn, H., Butaye, J., Dumortier, M., Hermy, M., & Lust, N. (2001). Effects of age and distance on the composition of mixed deciduous forest fragments in an agricultural landscape. *Journal of Vegetation Science*, 12, 635–642. http://dx.doi.org/10.2307/3236903

Jiménez, M. D., Ruíz-Capillas, P., Mola, I., Pérez-Corona, E., Casado, M. A., & Balaguer, L. (2013). Soil development at the roadside: A case study of a novel ecosystem. *Land Degradation & Development & Development*, 24(6), 564–574. http://dx.doi.org/10.1002/ldr.1157

Jodoin, Y., Lavoie, C., Villeneuve, P., Theriault, M., Beaulieu, J., & Belzile, F. (2008). Highways as corridors and habitats for the invasive common reed *Phragmites australis* in Quebec, Canada. *Journal of Applied Ecology*, 45(2), 459–466. http://dx.doi.org/10.1111/j.1365-2664.2007.01362.x

Johnson, J. B., & Omland, K. S. (2004). Model selection in ecology and evolution. *Trends in Ecology & Evolution*, 19(2), 101–108. http://dx.doi.org/10.1016/j.tree.2003.10.013

Jones, C., Lawton, J., & Shachak, M. (1994). Organisms as ecosystem engineers. *Ecosystem Management*, 69, 373–386. http://dx.doi.org/10.1007/978-1-4612-4018-1_14

Lugo, A. E., & Gucinski, H. (2000). Function, effects, and management of forest roads. *Forest Ecology and Management*, 133(3), 249–262. http://dx.doi.org/10.1016/S0378-1127(99)00237-6

Maestre, F. T., Quero, J. L., Gotelli, N. J., Escudero, A., Ochoa, V., Delgado-Baquerizo, M., et al. (2012). Plant species richness and ecosystem multifunctionality in global drylands. *Science*, 335(6065), 214–218. http://dx.doi.org/10.1126/science.1215442

Magro, S., Jiménez, M. D., Casado, M. A., Mola, I., Arenas, J. M., Martín-Duque, J. F., et al. (2014). Community ontogeny at the roadside: Critical life-cycle events throughout a sequential process of primary colonization. *Applied Vegetation Science*, 17(3), 493–503. http://dx.doi.org/10.1111/avsc.12095

Manning, A. D., Lindenmayer, D. B., & Fischer, J. (2006). Stretch goals and backcasting: Approaches for overcoming barriers to large-scale ecological restoration. *Restoration Ecology*, 14(4), 487–492. http://dx.doi.org/10.1111/j.1526-100X.2006.00159.x

Mola, I., Jiménez, M. D., López-Jiménez, N., Casado, M. A., & Balaguer, L. (2011). Road-side reclamation outside the revegetation season: Management options under schedule pressure. *Restoration Ecology*, 19(1), 83–92. http://dx.doi.org/10.1111/j.1526-100X.2009.00547.x

Münzbergová, Z., & Herben, T. (2005). Seed, dispersal, microsite, habitat and recruitment limitation: identification of terms and concepts in studies of limitations. *Oecologia*, 145(1), 1–8. http://dx.doi.org/10.1007/s00442-005-0052-1

Nathan, R., Horn, H. S., Chave, J., & Levin, S. A. (2002). Mechanistic models for tree seed dispersal by wind in dense forests and open landscapes. In D. J. Levey, W. R. Silva, & M. Galetti (Eds.), *Seed dispersal and frugivory: Ecology, evolution and conservation* (pp. 69–82).

Nathan, R., & Muller-Landau, H. C. (2000). Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology & Evolution*, 15(7), 278–285. http://dx.doi.org/10.1016/S0169-5347(00)01874-7

National Geographic Institute of Spain. (2011). *PNOA, Plan Nacional de Ortofotografía Aérea*. Retrieved from http://www.ign.es/PNOA/

Ninyerola, M., Pons, X., & Roure, J. (2005). *Atlas Climático Digital de la Península Ibérica Metodología y aplicaciones en bioclimatología y geobotánica*. Bellaterra: Universidad Autónoma de Barcelona.

Novák, J., & Prach, K. (2003). Vegetation succession in basalt quarries: Pattern on a landscape scale. *Applied Vegetation Science*, 6, 111–116. http://dx.doi.org/10.1111/j.1654-109X.2003.tb00570.x

Olander, L. P., Scatena, F., & Silver, W. L. (1998). Impacts of disturbance initiated by road construction in a subtropical cloud forest in the Luquillo Experimental Forest, Puerto Rico. *Forest Ecology and Management*, 109(1–3), 33–49. http://dx.doi.org/10.1016/S0378-1127(98)00261-8

Parker, V. T. (1997). The scale of successional models and restoration objectives. *Restoration Ecology*, 5(4), 301–306. http://dx.doi.org/10.1046/j.1526-100X.1997.00031.x

Patton, D. (1975). A diversity index for quantifying habitat edge. *Wildlife Society Bulletin*, 3(4), 171–173.

Pausas, J. G., Bonet, A., Maestre, F. T., & Climent, A. (2006). The role of the perch effect on the nucleation process in Mediterranean semi-arid oldfields. *Acta Oecologica*, 29(3), 346–352. http://dx.doi.org/10.1016/j.actao.2005.12.004

Pons, X. (2010). *MiraMon. Geographical information system and remote sensing software. Versión 7*. Bellaterra: Centre de Recerca Ecològica i Aplicacions Forestals (CREAF).

Prach, K., & Hobbs, R. (2008). Spontaneous succession versus technical reclamation in the restoration of disturbed sites. *Restoration Ecology*, 16(3), 363–366. http://dx.doi.org/10.1111/j.1526-100X.2008.00412.x

Prach, K., Pysek, P., & Jarosík, V. (2007). Climate and pH as determinants of vegetation succession in Central European man-made habitats. *Journal of Vegetation Science*, 18, 701–710. http://dx.doi.org/10.1111/j.1654-1103.2007.tb02584.x

R Development Core Team. (2012). *R: A language and environment for statistical computing*. Vienna, Austria. Retrieved from http://www.r-project.org/

Rey Benayas, J. R., Bullock, J. M., & Newton, A. C. (2008). Creating woodland islets to reconcile ecological restoration, conservation, and agricultural land use. *Frontiers in Ecology and the Environment*, 6, 329–336. http://dx.doi.org/10.1890/070057

Schmitz, M. F., Sánchez, I. A., & de Aranzabal, I. (2007). Influence of management regimes of adjacent land uses on the woody plant richness of hedgerows in Spanish cultural landscapes. *Biological Conservation*, 135(4), 542–554. http://dx.doi.org/10.1016/j.biocon.2006.10.053

Singh, A. N., Raghubanshi, A. S., & Singh, J. S. (2002). Plantations as a tool for mine spoil restoration. *Current Science*, 82(2), 1436–1441.

Spooner, P. G. (2005). Response of Acacia species to disturbance by roadworks in roadside environments in southern New South Wales, Australia. *Biological Conservation*, 122, 231–242. http://dx.doi.org/10.1016/j.biocon.2004.07.012

Spooner, P. G., Lunt, I. D., Briggs, S. V., & Freudenberger, D. (2004). Effects of soil disturbance from roadworks on roadside shrubs in a fragmented agricultural landscape. *Biological Conservation*, 117(4), 393–406. http://dx.doi.org/10.1016/j.biocon.2003.08.003

Spooner, P., & Smallbone, L. (2009). Effects of road age on the structure of roadside vegetation in south-eastern Australia. *Agriculture Ecosystems & Environment*, 129(1–3), 57–64. http://dx.doi.org/10.1016/j.agee.2008.07.008

Svoray, T., Mazor, S., & Bar (Kutiel), P. (2006). How is shrub cover related to soil moisture and patch geometry in the fragmented landscape of the Northern Negev desert? *Landscape Ecology*, 22(1), 105–116. http://dx.doi.org/10.1007/s10980-006-9004-3

Tikka, P., Högmander, H., & Koski, P. (2001). Road and railway verges serve as dispersal corridors for grassland plants. *Landscape Ecology*, 16, 659–666. http://dx.doi.org/10.1023/A:1013120529382

Tikka, P., Koski, P., Kivelä, R., & Kuitunen, M. (2000). Can grassland plant communities be preserved on road and railway verges? *Applied Vegetation Science*, 3, 25–32. http://dx.doi.org/10.2307/1478915

Walker, L. R., Velázquez, E., & Shiels, A. B. (2009). Applying lessons from ecological succession to the restoration of landslides. *Plant Soil*, 324(1–2), 157–168. http://dx.doi.org/10.1007/s11104-008-9864-1

Wilby, A., & Shachak, M. (2004). Shrubs, granivores and annual plant community stability in an arid ecosystem. *Oikos*, 106, 209–216. http://dx.doi.org/10.1111/j.0030-1299.2004.13085.x

Yao, J., Holt, R., Rich, P., & Marshall, W. (1999). Woody plant colonization in an experimentally fragmented landscape. *Ecography*, 22, 715–728. http://dx.doi.org/10.1111/j.1600-0587.1999.tb00521.x

Zeng, S.-L., Zhang, T.-T., Gao, Y., Ouyang, Z.-T., Chen, J.-K., Li, B., et al. (2011). Effects of road age and distance on plant biodiversity: A case study in the Yellow River Delta of China. *Plant Ecology*, 212(7), 1213–1229. http://dx.doi.org/10.1007/s11258-011-9899-x

Capítulo 3

The influence of site factors and proximity of adjacent vegetation on tree regeneration into roadslopes

J.M. Arenas, A. Lázaro-Lobo, I. Mola, A. Escudero, M.A. Casado

The influence of site factors and proximity of adjacent vegetation on tree regeneration into roadslopes

J.M. Arenas [a,*], A. Lázaro-Lobo [a], I. Mola [b], A. Escudero [c], M.A. Casado [a]

[a] Departamento de Ecología, Universidad Complutense de Madrid, 28040 Madrid, Spain
[b] Research, Development and Innovation (R&D) Service, Obrascón Huarte Lain, S.A. (OHL), 28046 Madrid, Spain
[c] Unidad de Biodiversidad y Conservación, Departamento de Biología y Geología, Universidad Rey Juan Carlos, Móstoles, 28933 Madrid, Spain

ABSTRACT

Many studies have shown evidence of very rapid natural colonization of trees on roadslopes. Tree colonization on roadslopes can be a useful tool in the ecological restoration of these degraded areas. However, little is known about the characteristics of the tree species capable of colonizing these novel habitats. Moreover, it is necessary to know how tree species respond to the two main limitations in these areas: microsite availability (i.e., roadslope characteristics) and seed arrival, which is related to propagule source, dispersion vector and landscape characteristics. The present study aims to investigate the natural colonization of tree species on roadslopes, as well as the factors determining their occurrence. We identified all tree individuals on 150 roadslopes, along 51 km of a motorway. A total of 1143 individuals belonging to 18 species was recorded. Most individuals found resulted from a natural colonization process, although we found various fruit trees (present in 7 roadslopes) and *Robinia pseudoacacia* (2 roadslopes), which are probably associated with unintentional human-mediated seed dispersal. Only the six most abundant species were analysed in detail: *Populus nigra, Quercus ilex, Quercus pyrenaica, Fraxinus angustifolia, Salix* spp. and *Ulmus pumila*. Each roadslope was characterized both by site variables and by surrounding variables. We analysed the effect of the descriptive variables on the occurrence and density of each species on the roadslopes, and we subsequently used decision trees (classification and regression trees) to analyse the combined effect of the different predictors considered. Our results show successful tree colonization on the roadslopes, although they appear to indicate limitations to colonization associated with the availability of propagules. Furthermore, tree species dispersed by animals required a continuous flow of seeds favoured by an appropriate community of seed dispersers and a suitable landscape structure. By contrast, wind-dispersed tree species basically need favourable site characteristics on the roadslopes.

1. Introduction

Road construction, especially of motorways, generates many roadcuts and embankments. These usually require restoration measures to achieve a two-fold goal: soil stabilization and environmental integration. Current roadslope restoration strategies include very costly measures such as topsoil spreading, hydroseeding with commercial seeds of fast-growing herbaceous plant species (Mola et al., 2011), and in some cases, low density planting of tree seedlings and shrubs. These plantings are typically performed for aesthetic purposes, and soil stabilization (Singh et al., 2002), but they can also facilitate the establishment of other species by ameliorating abiotic conditions (i.e., soil nutrients and water availability) (Bruno et al., 2003; Gómez-Aparicio et al., 2004). Moreover, plantings are expected to provide local seed sources and to serve as attractors of seed-dispersal vectors, thus increasing connectivity between remnant habitats and fragments at the landscape scale (Rey Benayas et al., 2008). However, woody species introduced in roadside areas often do not adapt well to the local environment due to the extreme abiotic conditions generated by the construction process (Hartley, 2002). This fact translates into higher costs for the companies responsible for roadside maintenance and conservation. As an alternative to plantations, recent studies have shown evidence of very rapid natural colonization of trees on roadslopes (Arenas et al., 2015; Coulson et al., 2013). If this is the case, this natural colonization could be sufficient to meet the objectives assigned to plantings in roadslopes.

Natural colonization of novel roadside habitats is subject to two main limitations: seed arrival and microsite availability (Münzbergová and Herben, 2005). Several studies suggest that seed banks on roadslopes are seriously depleted and irrelevant. This implies that the seeds of most species arrive from off the roadslopes (Bochet et al., 2007; Mola et al., 2011). As a consequence, wind-dispersed species tend to be fast colonizers of these new habitats (Bullock and Clarke, 2000; Campbell et al., 2003; Donath et al., 2003), with herbaceous wind-dispersed species usually over-represented on roadslopes, at least in the first years after construction (Bochet et al., 2007). Otherwise, animal-dispersed plants depend largely on the activity of seed dispersers (Jordano and Godoy, 2002). Except for exceptional cases (e.g., the existence of perches or trees bordering the roadside area), new roadsides are not attractive to most birds or other animal dispersers (Cuperus et al., 1996; Verdú and García-Fayos, 1996), which delays the entrance of animal-dispersed plants to the roadslopes. Nonetheless, seed dispersal by birds is critical for effective colonization of degraded areas (Bonet, 2004; Méndez et al., 2008). In addition, landscape configuration is critical for the arrival of seeds to low quality and novel patches from surrounding areas (Turner et al., 2001; Hersperger and Forman 2003). In the case of wind-dispersed species, landscape characteristics determine changes in wind speed and direction (Bohrer et al., 2008; Pounden et al., 2008; Schurr et al., 2008), which condition the arrival of wind-dispersed seeds to roadslopes. In the case of species dispersed by animals, it is expected that roadslopes can benefit from proximity to high-quality habitat remnants (e.g., forested areas), allowing for passive restoration mechanisms (Zamora et al., 2010). These high-quality habitats can provide an abundant and diverse source of both propagules and dispersers (Herrera et al., 2011; Levey et al., 2008; Torre et al., 2015; Wydhayagarn et al., 2009). Nevertheless, they are strongly limited by the distance, the degree of adjacency and the nature of surrounding vegetation to the roadslope (Zamora et al., 2010).

Seed arrival to roadslopes under Mediterranean climate conditions is insufficient to ensure successful colonization (Tormo et al., 2006). Microsite factors such as water availability, physical-chemical parameters, nutrient resources and biotic interactions, must be taken into account (Bochet and García-Fayos, 2004; de la Riva et al., 2011; Münzbergová, 2004). Microsite limitations are related to the characteristics of each roadslope (from here on, "site variables"): age, type (i.e., embankment or roadcut), soil and lithology, steepness of the slope, aspect and area of the roadslopes, which are thought to affect the establishment of long-term viable plant communities (Arenas et al., 2015; Bochet and García-Fayos, 2004; Cano et al., 2002; de la Riva et al., 2011; Deckers et al., 2005; Tormo et al., 2009).

To explicitly consider the role of natural tree colonization in roadslope restoration, knowledge of the factors affecting this process is critical. Success in colonization can be affected by the existence of both appropriate mechanisms allowing seed arrival and favourable microsites for the germination and recruitment of trees. With this in mind, the aims of this study were: a) to describe the diversity (both taxonomic and functional) of trees able to colonize roadslopes in an ample territory in Central Spain and b) to analyse the influence that both microsite characteristics and the surrounding landscape have on this colonization process. It is therefore vital to answer the following questions: What tree species are able to colonize roadslopes? Do the characteristics of the surrounding landscape affect the colonization ability of each species? Is the arrival of seeds limited by the existence of seed sources in nearby areas? Does successful establishment depend on the physical characteristics of the roadslope? All of this will elucidate the suitability of natural succession and passive restoration as a mechanism for restoring degraded ecosystems (Prach and Hobbs, 2008), and in

particular, for the restoration of woody vegetation on roadslopes (Arenas et al., 2015).

2. Material and methods

2.1. Study area

The study was conducted on the A1 motorway, in the Castilla y León autonomous region, central Spain (Fig. 1). We selected a 54 km section between the kilometric point 99 (41° 11′ N, 3° 35′ W) and 153 (41° 36′ N, 3° 42′ W). The selected road section passes through a gentle hilly region that has determined the necessary construction of many roadslopes. Moreover, it passes through a territory in which agricultural and forestry areas alternate, making it an ideal scenario for evaluating the influence of landscape in woody plant colonization processes. This area has a relatively uniform continental Mediterranean climate, with an average annual temperature of 11.2 °C and a mean annual rainfall of 480 mm. The landscape is profoundly humanized and characterized by extensive cereal crops, grasslands, scrublands and forests, both natural (e.g., holm oaks, Pyrenean oaks) and planted.

2.2. Field characterization

Among the different components of road verges, we focused on roadslopes because they provide a more favourable testing ground for colonization processes as they are isolated patches that are spatially well-defined and devoid of vegetation after construction. We selected 150 roadslopes, both roadcuts (56) and embankments (94), with a height of at least 2 m. Roadcuts are roadslopes resulting from excavation, whereas embankments are constructed by compacting earth and eventually applying topsoil. Some stretches of this highway, which are evenly distributed along the studied motorway section, were remodelled between 2009 and 2011. This implies that some roadslopes were newly constructed or modified by removing all existing vegetation, whereas others remained intact (of an unknown age, but at least 20 years since their construction). This constitutes a unique opportunity because it provides a specific consideration of time in our observational study. Thus, we sampled 22 new roadcuts, 34 old roadcuts, 22 new embankments and 72 old embankments. Besides age category, other site variables were considered on each roadslope: aspect (east or west), altitude at the base of the roadslope, slope, and area, as well as the dominant lithology, namely acid substrate (e.g., granite, gneiss, sandstone, quartzite) or basic substrate (e.g., limestones, marls). In order to calculate the area, we also measured length and height at various points of each roadslope.

On each roadslope we counted all individuals of each tree species. We excluded planted individuals, which were identified taking into consideration the existence of regular spatial patterns, similar sizes (i.e., ages) or other indications of plantation. This criterion involved the exclusion of less than 1% of individuals identified. For each individual, the distance to the nearest conspecific adult tree was measured. Finally, for each roadslope, the density of individuals of each species (number of individuals per hectare) was calculated, taking into account roadslope area. Sampling was conducted in October 2012, when the herbaceous vegetation was dry, which enabled us to differentiate and easily detect woody plants.

The influence of the matrix close to each roadslope, which constitutes a critical factor, was determined both with aerial photographs (considering vegetation types) and field surveys (differentiating at the species level). The aerial photographs considered were taken in 2009 for the Aerial Orthophotography National Plan of the National Geographic Institute of Spain (2011) and presented a pixel resolution of 0.5 m. At a large scale, we considered a dis-
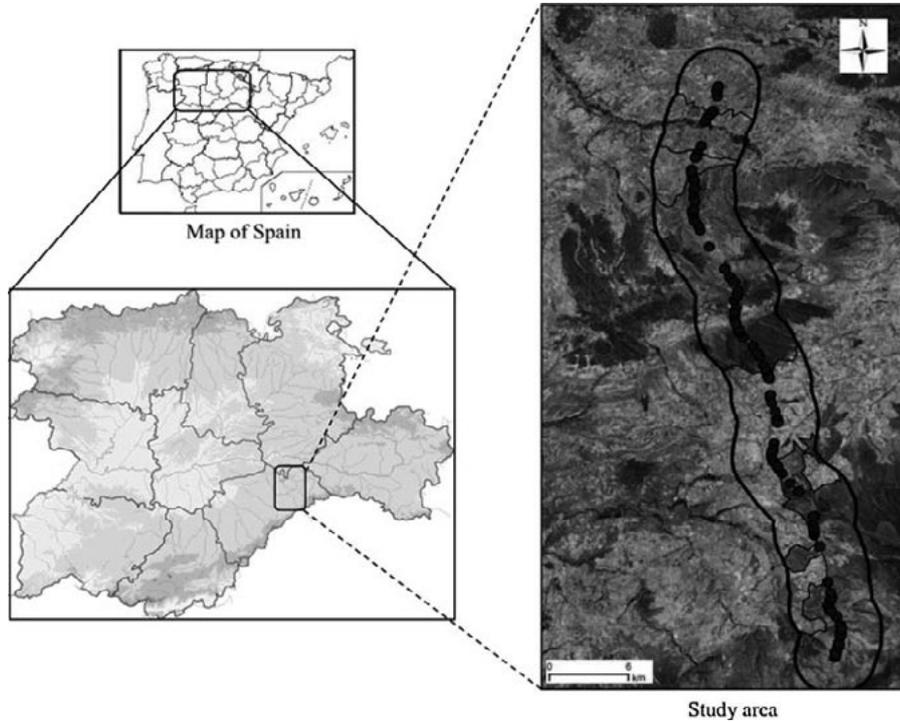
**Fig. 1.** Study area along the A1 motorway from kilometric point 99–153. The studied area is marked with a thick line and corresponds to 3 km on each side of the road. Points indicate sampled roadslopes and thin lines separate the sectors defined as forestry or agricultural use.
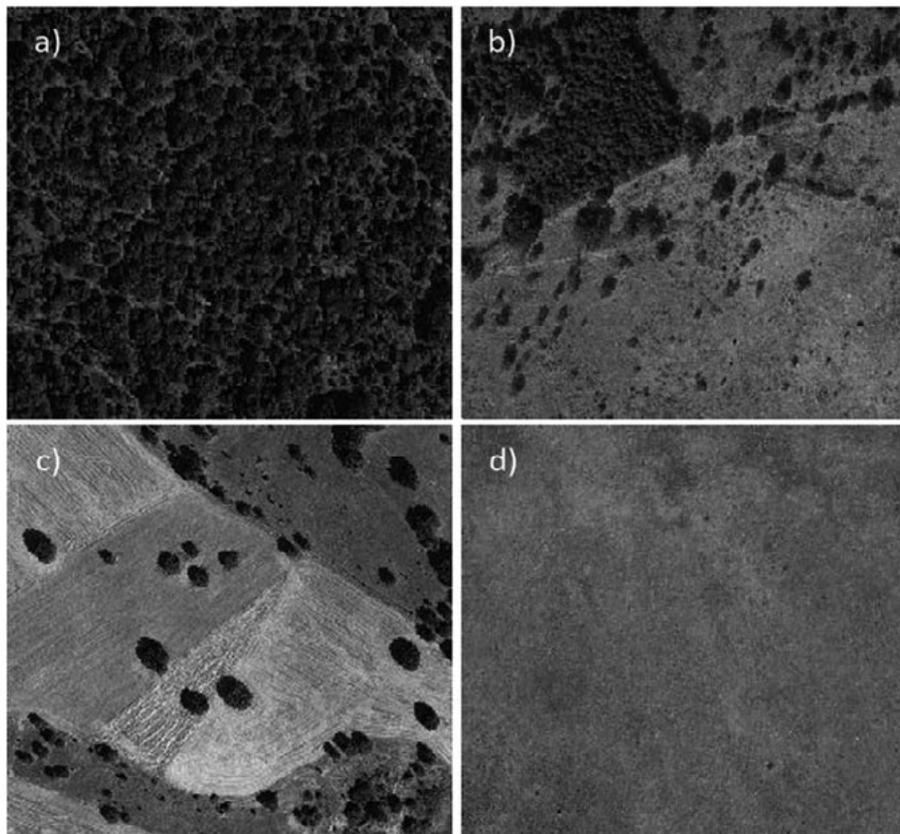

Fig. 2. Landscape structure. The pictures show representative areas of landscape with forest (a), woods (b), scattered trees (c) and treeless (d).

tance of up to 1 km from the road, assigning the predominant type of landscape (agricultural or forestry) to each roadslope. We also measured both tree cover and landscape structure at three concentric distances: short (0–20 m), medium (20–150 m) and long (150–500). Percentage of tree cover in each of the three concentric belts was estimated by means of aerial photography and using a grid in the open source tool Quantum GIS (QGIS Development Team, 2013). Landscape structure considered the spatial distribution of the trees and was categorized into 4 levels: without trees, scattered trees, scattered woods and dominance of woods (Fig. 2). In the field, the presence of each tree species was recorded at two concentric distances: short (0–20 m) and medium (20–150 m). The density of each species (number of individuals per hectare) at the shorter distance was also calculated, using the number of individuals sampled in the field survey and the area in the short-distance zone.

2.3. Data analyses

We considered both occurrence and density of each species on the roadslopes. Occurrence provides information on the suitability of a roadslope with regard to receiving seeds, while density reflects the influence of different factors upon the success of colonization.

In the case of the occurrence data, we used contingency tables and Fisher's exact test to analyse the effect of categorical soil variables of the roadslopes: roadslope type (roadcut vs embankment), roadslope age (new vs old), aspect (east vs west) and lithology (acid substrate vs basic substrate). Similarly, we tested the influence of the surrounding matrix: type of landscape (agricultural vs forestry) and landscape structure (without trees, scattered trees, scattered woods or dominance of woods). The influence of the continuous variables recorded from roadslopes (i.e., slope, area and elevation) and from the surrounding matrix (tree cover at short, medium and long distance) was tested by means of binomial generalized linear models.

In the case of the density data, we employed the Mann-Whitney test to analyse the effect of roadslope type, roadslope age, aspect, lithology and type of landscape in the surroundings. For the multicategorical variable –landscape structure- we used the Kruskal-Wallis test. The influence of continuous variables (i.e., slope, area, elevation and tree cover at short, medium and long distance) was tested with Spearman correlations.

The influence of the distance to the conspecific adult trees was analysed in two ways. On the one hand, we estimated the distance of each individual on the roadslope to the nearest adult conspecific tree. We then calculated the cumulative distribution of the minimum distances for each species and determined the quartiles corresponding to 25% (Q25), 50% (Q50) and 75% (Q75) of the individuals. On the other hand, the relationships between the presence or absence of each species on the roadslopes and in their surrounding area at short (0–20) and medium distance (20–150) were analysed with the use of the Fisher's exact test. We also analysed the relationship between density of each species on the roadslope and density at a short distance, as well as the relationship between the same density on the roadslope and the presence at a medium distance, by means of the Spearman correlation and the Mann-Whitney test, respectively.

We performed Fisher's exact test, Mann-Whitney tests and binomial generalized linear models using the "fisher.test ()", "wilcox.test ()", and "glm (..., family = binomial)" functions in the base R packages, respectively (R Core Team, 2015). We performed Spearman correlations using the "correlation (..., method = "spearman")" function in the agricolae R packages (de Mendiburu, 2014). When the relationships between the occurrence of each species on the roadslopes and landscape structure were significant, we conducted a post-hoc analysis to test significant dif-

Table 1
List of the tree species in the roadslope survey.

Species	Individuals	Number of roadslopes
Populus nigra L.	631	56
Quercus ilex subsp. *ballota* (Desf.) Samp.	151	35
Quercus pyrenaica Wild.	100	22
Robinia pseudoacacia L.	54	2
Fraxinus angustifolia Vahl.	38	10
Salix spp.	34	11
Ulmus pumila L.	31	10
Pyrus communis L.	30	1
Prunus dulcis (Mill.) D. A. Webb	22	2
Pinus pinaster Ait.	16	8
Juniperus thurifera L.	14	7
Malus domestica Borkh	8	4
Quercus faginea Lam.	6	3
Crataegus monogyna Jacq.	2	2
Pinus pinea L.	2	1
Pinus sylvestris L.	2	2
Juniperus oxycedrus L.	1	1
Prunus persica (L.) Batsch	1	1
TOTAL	1143	

ferences among all pairs of populations using the "chisq.post.hoc (..., test = c('fisher.test'))" function in the fifer R packages (Fife, 2014). We performed the Kruskal-Wallis test with multiple comparison of structures using the "kruskal" function in the agricolae R packages (de Mendiburu, 2014).

Finally, we used decision trees (classification and regression trees) to analyse the combined effect of the different predictors considered for each of the six species modelled. Classification and regression trees are nonparametric techniques well suited for analysing complex ecological data and non-additive effects, and they enable the importance of the variables considered to be hierarchized. Data are split into increasingly homogenous groups based on the predictor variable at each split, which explains the greatest deviance from the dataset. Classification trees are designed for dependent variables that take a finite number of unordered values, whereas regression trees are for dependent variables that take continuous or ordered discrete values. We fitted the modelled trees by considering either the occurrence of the species on the roadslope (classification tree) or species density on the roadslope (regression tree) as response variables. Predictors were: type (embankment or roadcut), age (new or old), lithology (acid or basic), altitude, and slope, density of conspecific trees at short distance (0–20 m), presence of conspecific trees at short and medium distances (0–20 m and 20–150 m), the predominant type of landscape (agricultural or forestry) and percentage of tree cover and landscape structure at three distances, short (0–20 m), medium (20–150 m) and long (150–500). We fitted the six classification and the six regression trees with SPSS 19 (IBM SPSS Statistics: Armonk, NY, USA) using the CHAID algorithm.

Given the constraints of the analysis used in this study, we only considered the six species present in at least in 10 roadslopes: *Quercus ilex, Quercus pyrenaica, Populus nigra, Fraxinus angustifolia, Ulmus pumila* and *Salix* spp.

3. Results

A total of 1143 individuals of 18 species were found in the roadslopes (Table 1). Some species, like *Populus nigra, Quercus ilex* and *Quercus pyrenaica*, were especially frequent and abundant on many roadslopes. By contrast, species such as *Juniperus oxycedrus, Prunus persica, Pinus pinea* or *Crataegus monogyna*, appeared sporadically. *Pyrus communis* and *Robinia pseudoacacia* presented high local abundances, but were only located on one and two roadslopes, respectively.

Table 2
Relationship between site variables of the roadslope and the density of individuals of each species. Type of slope (roadcut *vs* embankment), age (new *vs* old), aspect (east *vs* west), lithology (acid *vs* basic), slope and altitude were considered. For the discrete variables we analysed the relationship using the Mann-Whitney test (U), while for the continuous variables we used the Spearman correlation (r). Bold values indicate significant differences (p < 0.05).

	Type		Age		Aspect		Slope		Altitude		Lithology	
	U	p	U	p	U	p	r	p	r	p	U	p
Quercus ilex	2276	0.062	1685	**<0.001**	2587	0.279	0.087	0.291	0.134	0.101	1994	0.0894
Quercus pyrenaica	2363	0.089	1918	**0.005**	2632	0.304	0.037	0.656	0.329	**<0.001**	1598	**0.006**
Populus nigra	2404	0.308	1808	**0.013**	2443	0.121	−0.109	0.183	0.240	**0.003**	1625	0.073
Fraxinus angustifolia	2497	0.225	2112	**0.036**	2742	0.610	−0.119	0.148	0.228	**0.005**	1802	0.078
Ulmus pumila	2425	0.062	2185	0.159	2775	0.824	−0.164	**0.044**	0.229	**0.005**	1802	0.078
Salix spp.	2465	0.151	2307	0.816	2795	0.967	−0.117	0.155	0.160	0.051	1926	0.648

3.1. Factors associated with the roadslope

Except in the case of the decision trees, the results for the six most frequent species analysed in detail were almost identical for occurrence and density. Therefore, we only present results for density (see Supplementary material for occurrence results). Considering the set of factors related to the characteristics of the roadslopes, age (new or old) had a significant and positive effect on four of the six species: *Q. ilex, Q. pyrenaica, P. nigra* and *F. angustifolia* (Tables 2 and S1). By contrast, the type (embankment or roadcut) and the aspect of the roadslopes were not significant in any case. Furthermore, slope was only significant for *U. pumila*, which prefers gentle slopes, and altitude was significant in the case of *Q. pyrenaica, P. nigra, F. angustifolia,* and *U. pumila*, as all of these showed an increase in density with elevation. *Q. pyrenaica* was the only species associated with a specific lithology, appearing only in areas with acidic soils.

3.2. Factors associated with the surrounding area

Both occurrence and density on the roadslope showed a significant and positive relationship with the presence of conspecific adult individuals at medium distance (Tables 3 and S2). At short distances (0–20 m), *Q. ilex, Q. pyrenaica, P. nigra* and *F. angustifolia*

Table 3
Relationship between density of each species on the roadslopes and density at short distances, and relationship between density on the roadslopes and occurrence of species at medium distances. We analysed these relationships using the Spearman correlation and the Mann-Whitney test, respectively. Bold values indicate significant differences (p < 0.05). All significant relationships correspond to positive associations.

	Density at 0–20 m	Presence at 20–150 m
Quercus ilex	**<0.001**	**<0.001**
Quercus pyrenaica	**<0.001**	**<0.001**
Populus nigra	**<0.001**	**<0.001**
Fraxinus angustifolia	**0.009**	**<0.001**
Ulmus pumila	0.643	**<0.001**
Salix spp.	0.242	**0.001**

presented a significant and positive correlation between density on the roadslopes and density in the adjacent areas (Table 3). The distribution of the distance to the nearest conspecific adult tree was different for each species (Fig. 3). *Q. pyrenaica* and *Q. ilex* individuals were concentrated at a short distance from the adult tree. *Salix* spp. and *Fraxinus angustifolia* exhibited an analogous pattern, with individuals concentrated at an intermediate distance. *P. nigra* showed higher distances from conspecific adult trees. Finally, the species with the most distant potential seed sources was *U. pumila*.

Landscape type in the surroundings of the roadslopes affected the occurrence and density of almost all species studied, except *Salix* spp. (Tables 4 and S3a). They preferred forested areas to agricultural landscapes. Tree cover at different distances (0–20 m, 20–150 m, and 150–500 m) influenced the occurrence of *Q. ilex* and *Q. pyrenaica* (Table S3a), as well as the density of both *Quercus* and *P. nigra* (Table 4). This relationship was always positive. Furthermore, both *Quercus* species were also related to the landscape structure in the surrounding area. At short distances, the presence of trees was determinant, either scattered trees or woods, while at long distances the presence of forests was more significant (Tables 4 and S3b).

3.3. Decision trees

The classification trees for occurrence data showed a first split in all species determined by the presence of conspecific trees in the surrounding area (Fig. 4). In the case of *Q. ilex* and *Q. pyrenaica*, the presence of adult trees was significant at short distances (0–20 m) whereas for the other four species it was significant at medium distances (20–150 m). Moreover, the variables that determined the second split of the classification trees for *Q. ilex* and *Q. pyrenaica* were also the same: when adult trees of *Q. ilex* and *Q. pyrenaica* were present at short distances in the surrounding area, there was greater seedling density in older roadslopes. If they were absent, colonization was favoured by high tree cover values at medium or long distances (Fig. 4A and B). By contrast, roadslope age was not relevant for any of the other four species. *P. nigra* appeared to be determined only by the presence of conspecific trees in the sur-

Table 4
Influence of different variables related to the surrounding landscape in the density of individuals of each species on the roadslopes. Tree cover and landscape structure were evaluated at three distances from the road. The influence of landscape type (agricultural *vs* forestry) on the density of each species on the roadslopes was tested with the use of the Mann-Whitney test. The relationship between density on the roadslope and tree cover at short (0–20 m), medium (20–150 m) and long distances (150–500 m) was tested with the Spearman correlation. The influence of landscape structure (without trees, scattered trees, scattered woods or forest) upon density on the roadslope was tested with a Kruskal-Wallis test. The figures correspond with p-values. Bold values indicate significant differences (P < 0.05).

	Type of landscape	Tree cover			Structure		
		0–20	20–150	150–500	0–20	20–150	150–500
Quercus ilex	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**0.016**	0.06	**<0.001**
Quercus pyrenaica	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**0.005**	**0.005**	**0.005**
Populus nigra	**0.015**	**0.02**	0.056	**0.009**	0.195	0.202	0.092
Fraxinus angustifolia	**0.018**	0.385	0.144	0.811	0.333	0.071	0.463
Ulmus pumila	**0.018**	0.367	0.138	0.696	0.361	0.218	0.481
Salix spp.	0.547	0.727	0.483	0.934	0.933	0.346	0.247

Fig. 3. Cumulative frequency distribution of the distance from each individual on the roadslope to the nearest adult conspecific tree. For each species, the distance accumulating 25% (Q25, dashed line), 50% (Q50, thin line) and 75% (Q75, thick line) of individuals found in the roadslopes is marked. A: *Quercus ilex*, B: *Quercus pyrenaica*, C: *Populus nigra*, D: *Fraxinus angustifolia*, E: *Ulmus pumila*, F: *Salix* spp.
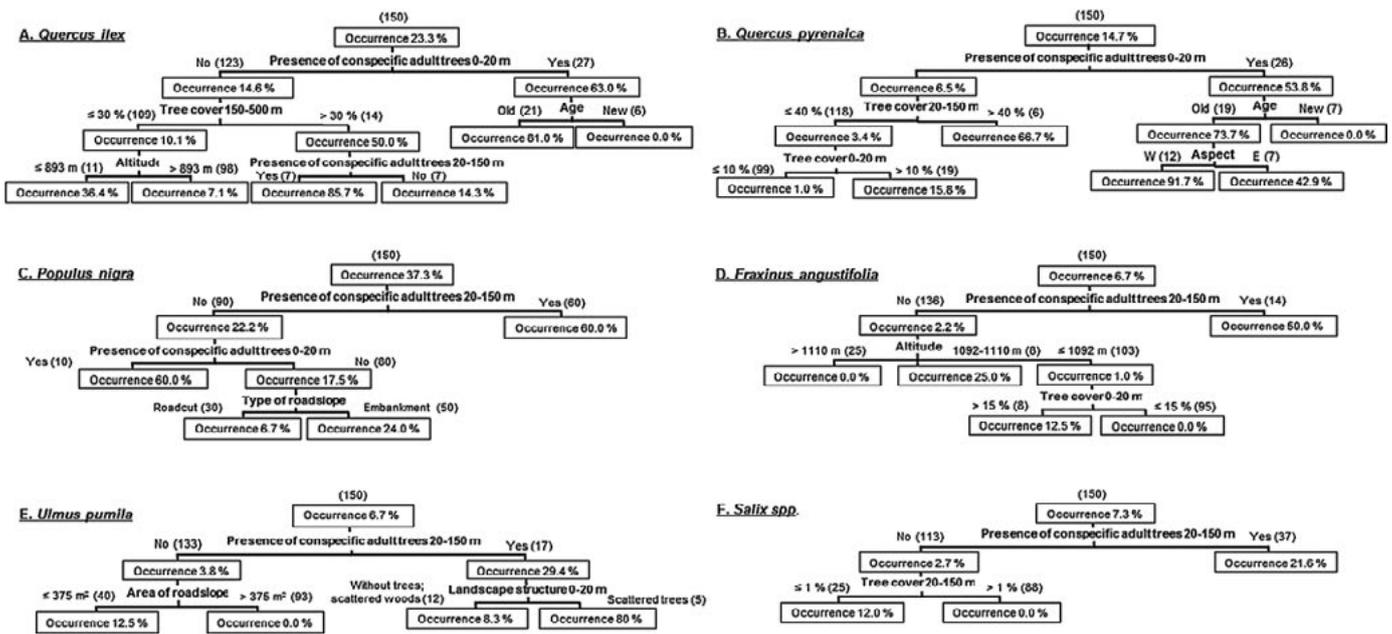
Fig. 4. Classification trees. A: *Quercus ilex*, B: *Quercus pyrenaica*, C: *Populus nigra*, D: *Fraxinus angustifolia*, E: *Ulmus pumila*, F: *Salix* spp.

rounding area, since in the absence of *P. nigra* at medium distances (20–150 m), the presence of *P. nigra* is critical at short distances (0–20 m; Fig. 4C). The variable associated with the second split was highly variable for *Fraxinus* (mean altitude; Fig. 4D), *Ulmus* (low roadslope area; Fig. 4E), and *Salix* (low tree cover at 20–150 m; Fig. 4F).

Regression trees for densities were idiosyncratic. In *Q. ilex* and *Q. pyrenaica*, the surrounding structure at long and medium distances constituted the most important factor (first or second split, respectively). *Q. ilex* reached its maximum density (176 individuals/ha) on roadslopes when forests existed in the surrounding area, with an intermediate tree cover at short distances (0–20 m; Fig. 5A). *Q. pyrenaica* reached the highest density (143 individuals/ha) when

density at short distances was high, and secondarily when there was forest at medium distances (Fig. 5B). The other four species showed more complex patterns, but they presented regression trees in which the presence of conspecifics at medium distances (20–150 m) was significant in some splits. This constituted the only variable for *Salix spp* (Fig. 5F). *P. nigra* also presented this variable as a first split, and altitude as the following one (Fig. 5C). These two variables were also the most important for *F. angustifolia*, although altitude determined the first split and presence of conspecific trees at medium distances determined the second one (Fig. 5D). Finally, the highest densities on roadslopes for *U. pumila* were determined by intermediate tree covers at medium distances (20–150 m), and
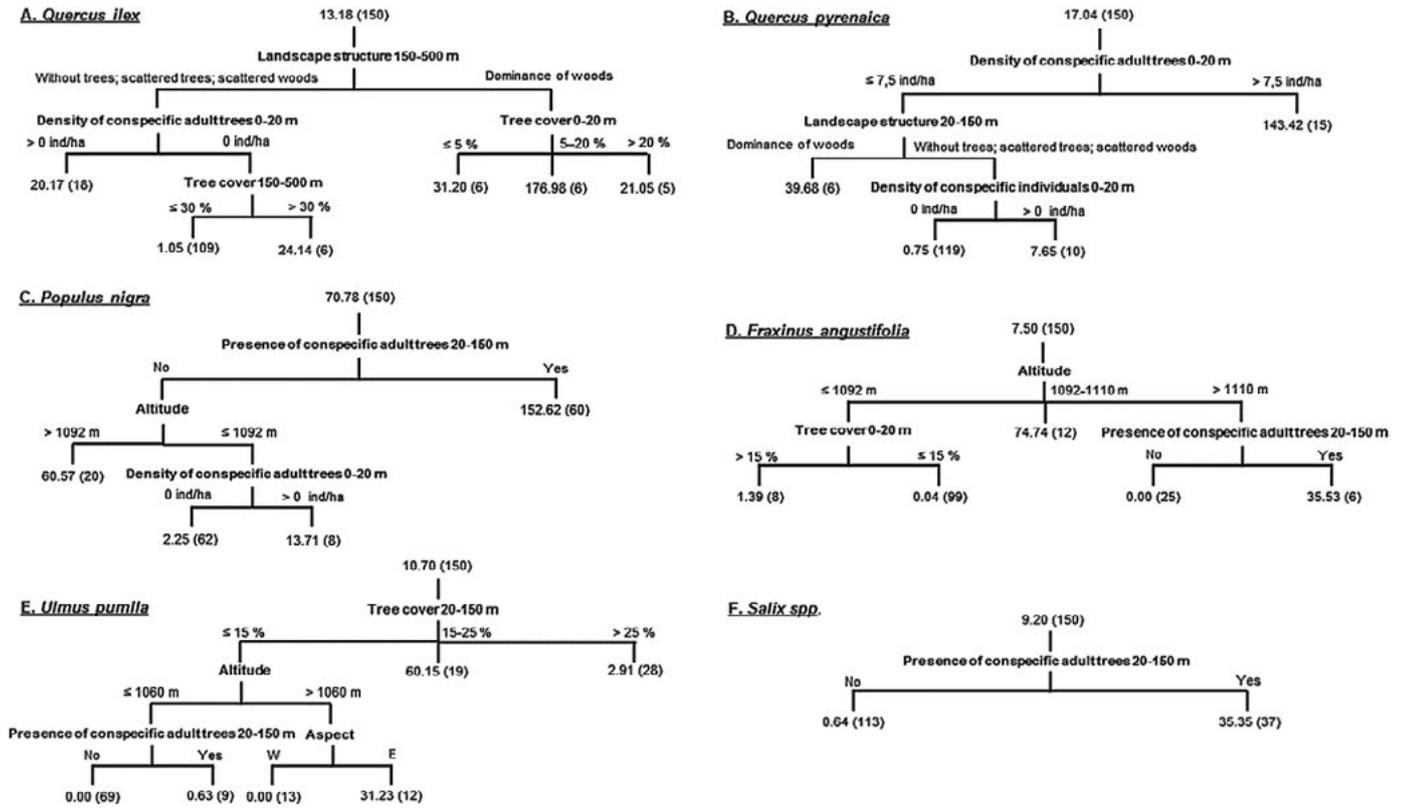
Fig. 5. Regression trees. A: *Quercus ilex*, B: *Quercus pyrenaica*, C: *Populus nigra*, D: *Fraxinus angustifolia*, E: *Ulmus pumila*, F: *Salix* spp.

secondly by the combination of high altitude and east-facing road-slopes (Fig. 5E).

4. Discussion

Our results show that a high number of tree species are able to reach and colonize roadslopes under very different landscape configurations and microsite features. Although some of the species, such as various fruit trees and *Robinia pseudoacacia*, are probably associated with unintentional human-mediated seed dispersal, most of the trees found are related to a natural colonization process. Natural colonization is idiosyncratic (species dependent) and related both to the characteristics of the roadslope itself and to the characteristics of the surrounding area (i.e., landscape structure and land use). These findings provide a complete view of the potential of roadslopes to be naturally colonized by trees (occurrence and density), as well as this colonization's dependence upon dispersal and establishment processes.

4.1. Unintentional human-mediated seed dispersal

Human-mediated seed dispersal is already recognised as an important mechanism in colonization (Pickering and Mount, 2010; von der Lippe et al., 2013; Wichmann et al., 2009). On roadsides, several studies have demonstrated potential dispersal by means of attachment of seeds or propagules to vehicles (Clifford, 1959; Taylor et al., 2012; Zwaenepoel et al., 2006) or simply due to the airflow of vehicles (von der Lippe et al., 2013). Unintentional human-mediated seed dispersal is also evident in our study, although it is different from that described in the literature. Firstly, we found several fruit trees, such as pear trees (*Pyrus communis*), apple trees (*Malus domestica*) and peach trees (*Prunus persica*),

which are likely associated with scraps of fruit thrown from vehicles, since no mother trees were found in the surrounding area. Secondly, there is a notably low occurrence (only two roadslopes), but a high local abundance of *Robinia pseudoacacia*. The species *R. pseudoacacia* is a common exotic species naturalized inland on the Iberian Peninsula and is included in the Catalogue of invasive species in Spain (Sanz-Elorza et al., 2004). This tree species regenerates both sexually through seeds and asexually through adventitious buds on stumps and roots (Kurokochi et al., 2010). However, we detected no sources of propagules in the surroundings and consequently, its presence is probably associated with arrival via earthworks conducted during road construction.

4.2. Natural dispersal and colonization

The six most abundant species arrived by means of natural dispersal processes. Surprisingly, these species cover an ample range of dispersal features, which leads us to conclude that no dispersal limitations exist, at least for this tree assemblage. Based on the size, shape and the existence of specialized structures in seeds, we identified three dispersal syndromes. The fruits of *Q. ilex* and *Q. pyrenaica* are large acorns (mean of 220 and 375 seeds/kg, respectively; Catalán 1991), which are passively dispersed under the mother canopies and more effectively by wildlife, particularly birds like magpies (*Pica pica*) and the European jay (*Garrulus glandarius*) (Gómez et al., 2003; Pons and Pausas, 2007; Siscart et al., 1999). On the other hand, close relatives *Populus nigra* and *Salix spp* have very small seeds (mean of 7,00,000 and 5,000,000 seeds/kg; Catalán, 1991), with a hairy pappus that facilitates long-distance dispersal by wind. Finally, the fruits of *Ulmus pumila* and *Fraxinus angustifolia* are samaras, with relatively large seeds (mean of 17,500 and 140,000 seeds/kg; Catalán, 1991), but with a wing which enables

dispersion by wind. Both *Quercus* trees presented the minimum distance to the closest possible mother tree (Fig. 3). This result suggests that species dispersal by animals poses more difficulties with regard to reaching the roadslopes than wind-dispersed tree species. This is in line with other studies, which have established that wind-dispersed species are over-represented in the flora of the roadslopes (Bochet et al., 2007). However, this feature did not seem to limit recruitment and colonization on roadslopes in our study system.

The abiotic characteristics of each roadslope pose some clues to seed germination and seedling establishment. Variables such as the roadslope type, age, aspect, slope and surface area of the roadslopes have been described as important determinants of colonization, although none of these variables have been, to our knowledge, sufficiently evaluated in relation to tree performance (Arenas et al., 2015; Bochet and García-Fayos, 2004; Cano et al., 2002; de la Riva et al., 2011; Tormo et al., 2009). Roadslope type (i.e., embankment or roadcut) is one of the main variables given attention in most studies of roadslope vegetation. The impressive constructive differences between roadcuts and embankments determine conspicuous ecological differences (soil conditions, nutrient availability, water availability, etc.) (Bochet and García-Fayos, 2004), which largely determine the herbaceous vegetation (Bochet et al., 2010, 2007). Strikingly, this difference did not affect tree occurrence or density. Only altitude and age were critical for most tree species. In a Mediterranean climate characterized by a severely dry summer, higher altitudes determine more benign summer temperatures and therefore more favourable habitat conditions.

Age since construction has been described as a key factor for woody colonization on roadslopes (Arenas et al., 2015; Olander et al., 1998; Spooner and Smallbone, 2009). In our case we found higher occurrences and densities on old roadslopes both for *Quercus* species and for *F. angustifolia*, together with higher densities of *P. nigra*. Two complementary mechanisms might be involved over time. Firstly, the likelihood of a species reaching a roadslope would be directly proportional to its age (Jacquemyn et al., 2001). This appears to be the principal determinant in the case of the two *Quercus* species, because the colonization process is less efficient. Secondly, the habitat carrying capacity of roadslopes tends to increase with time. Such an improvement would depend on the establishment of pioneer species, which would profoundly influence soil fertility, thus facilitating the establishment of more ecologically demanding species (García-Palacios et al., 2011; Jiménez et al., 2013). Additionally, soil amelioration would also result from an increase in the environmental heterogeneity deriving from the existence of gravitational movements of sediments, nutrients and water, which in turn create erosion and accumulation zones in roadcuts and embankments (Jiménez et al., 2013; Magro et al., 2014; Walker et al., 2009). This microsite amelioration is more decisive for species with seeds that reach roadslopes more easily, such as wind-dispersed species.

The configuration of habitat remnants in the surrounding area determines both propagule availability and probability of reaching degraded areas (Arenas et al., 2015; Bochet et al., 2007; Bochet and García-Fayos, 2015; Coulson et al., 2013). On one hand, vegetation from nearby natural fragments provides seeds to roadslopes (Bochet et al., 2007; Coulson et al., 2013; Mola et al., 2011). This effect seems patent for our six species, since they all show positive relationships between occurrence (and density) of each species on roadslopes and the presence of such species in the surrounding area (Tables 3 and S2). On the other hand, the vegetation matrix could influence dispersal processes by affecting the wind flow (Nathan et al., 2002) and movements of seed dispersers (Coulson et al., 2013; Pausas et al., 2006). For wind-dispersed species we found no evidence of a possible effect of landscape structure or tree cover in the surrounding area. On the contrary, for animal-dispersed species (*Q.*

ilex and *Q. pyrenaica*), both tree cover in the surrounding area and landscape structure were significant. This suggested that a greater amount of trees in the surrounding area favours the movements of forest birds, which are critical for the regeneration of these two species (Anderson and Shugart, 1974; Kluza et al., 2000).

Decision trees have enabled us to synthesize and hierarchize the factors considered. Variables from the surrounding area always constituted the main factors responsible for tree colonization on roadslopes. For both animal-dependent tree species (*Quercus*), their occurrence is associated with the presence of conspecific trees at short distances, especially if the roadslope is sufficiently old. However, the density of these tree species is more dependent on landscape structure (preference for wooded areas) and tree cover at short distances. These results suggest that colonization limitations are related both to the availability of propagules and especially to the existence of suitable animal dispersers. The presence of conspecific adult trees in the surroundings may be just enough for seeds to reach roadslopes, but this process is probably very slow, and therefore needs more time to become manifest. Successful colonization (evaluated by means of tree density on the roadslope) depends on a continuous flow of seeds favoured both by the appropriate community of birds and by a suitable landscape structure (Gómez, 2003). The seed flow of these acorns is known to be critically reduced below certain limits of appropriate habitat availability for bird dispersers (Collingham and Huntley, 2000; Malanson and Cairns, 1997; With, 2002). The importance of the factor "dominance of woods (forest)ät medium and long distances (*Q. pyrenaica* y *Q. ilex*, respectively) suggests that these phenomena of seed dispersal by birds are more intense and decisive in forest landscapes.

In the case of wind-dispersed tree species, factors related to the surrounding structure and seed sources were not significant to the colonization process. These factors were replaced by the availability of conspecific adult trees at medium distances as well as some critical features of the microsite. Remarkably, long-distance dispersal (Cain et al., 2000; Nathan, 2006) seems to be more important for wind-dispersed species than for the two species dispersed by birds (Fig. 3). Indeed, on 17.5% of roadslopes with *Populus nigra*, no conspecific adult trees were found in the surrounding area (radius of up to 150 m). Obviously, such long-distance dispersal can be directly favoured by the existence of more permeable landscapes (e.g. low tree cover) or indirectly through human-mediated dispersal of seeds by the airflow of vehicles (von der Lippe et al., 2013). In addition, the successful colonization of these wind-dispersed species increased on roadslopes located at higher altitudes. All the wind-dispersed trees, *Salix* spp., *U. pumila, P. nigra* and *F. angustifolia,* are species typical of relatively mesic climates, which are limited in Mediterranean Spain to more favourable habitats such as riparian forest or higher altitudes.

In summary, the present study showed that natural colonization in adverse novel habitats like roadslopes can be achieved not only by pioneer and wind-dispersed trees, but also by animal-dispersed ones. These more ecologically demanding animal-dispersed species require conspecific adult trees in the surrounding area, as well as a certain amount of time to arrive and settle on roadslopes. They have a vital need for dispersers in the surrounding area, as has also been indicated by other studies (Torre et al., 2015). By contrast, wind-dispersed species are less dependent on migration rates, but they do require favourable microsite characteristics on the roadslopes.

4.3. Lessons for ecological restoration of roadslopes

Our research concurs with a small number of studies sustaining that natural colonization of roadslopes is feasible, but depends on the availability of propagule sources and seed rain (Arenas et al., 2015; Bochet et al., 2007; Mola et al., 2011). Therefore, maintaining areas of natural vegetation in the vicinity of the roads enhances

the passive colonization of tree species on the roadslopes (see also Arenas et al., 2015; Bochet et al., 2007).

Establishment of native woody species can be considered to constitute a surrogate of restoration success (Prach and Hobbs, 2008). Here we have shown that natural colonization is effective for the establishment of different tree species on roadslopes, under a whole range of environmental conditions and landscape structures. In addition, our study highlights the existence of different strategies among trees. These can be grouped into large groups (two in our case) to propose interventions promoting natural colonization and passive restoration by focusing either on habitat suitability for animal species dispersers, or the availability of favourable microsites for wind-dispersed species. Therefore, restoration plans based on promoting natural colonization can, and should, be favoured, with more focus on groups of similar species than on individual ones.

The promotion of natural colonization by the surrounding vegetation as a useful restoration tool is a low-cost measure and has the advantage of increasing local diversity in these anthropic and novel ecosystems (Prach and Hobbs, 2008). Thus, practitioners can implement a new restoration paradigm, based on action strategies involving minimal intervention and focused on promoting natural colonization (Méndez et al., 2008). These actions are therefore appropriate where the objective entails establishing a vegetation cover requiring little or no maintenance, and which may involve multiple uses, such as biodiversity conservation or support of certain ecosystem services (Balaguer et al., 2011).

Acknowledgements

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecoleng.2017.01.007.

References

Anderson, S.H., Shugart, H.H., 1974. Habitat selection of breeding birds in an east Tennessee deciduous forest. Ecology 55, 828–837.

Arenas, J.M., Escudero, A., Magro, S., Balaguer, L., Casado, M.A., 2015. Woody colonization of road embankments: a large spatial scale survey in central Spain. Landscape Urban Plan. 141, 52–58, http://dx.doi.org/10.1016/j.landurbplan.2015.04.009.

Balaguer, L., Valladares, F., Mola, I., 2011. Restauración ecológica e infraestructuras de transporte: definiciones, problemas y desafíos. In: Valladares, F., Balaguer, L., Mola, I., Escudero, A., Alfaya, V. (Eds.), Restauración Ecológica de Áreas Afectadas Por Infraestructuras de Transporte. Bases Científicas Para Soluciones Técnicas. Fundacion Biodiversidad, Madrid, España.

Bochet, E., García-Fayos, P., 2004. Factors controlling vegetation establishment and water erosion on motorway slopes in Valencia, Spain. Restor. Ecol. 12, 166–174, http://dx.doi.org/10.1111/j.1061-2971.2004.0325.x.

Bochet, E., García-Fayos, P., 2015. Identifying plant traits: a key aspect for species selection in restoration of eroded roadsides in semiarid environments. Ecol. Eng. 83, 444–451, http://dx.doi.org/10.1016/j.ecoleng.2015.06.019.

Bochet, E., García-Fayos, P., Tormo, J., 2007. Road slope revegetation in semiarid Mediterranean environments. Part I: seed dispersal and spontaneous colonization. Restor. Ecol. 15, 88–96, http://dx.doi.org/10.1111/j.1526-100X.2006.00194.x.

Bochet, E., García-Fayos, P., Tormo, J., 2010. How can we control erosion of roadslopes in semiarid Mediterranean areas? Soil improvement and native plant establishment. Land Degrad. Dev. 121, 110–121, http://dx.doi.org/10.1002/ldr.911.

Bohrer, G., Katul, G., Nathan, R., Walko, R., 2008. Effects of canopy heterogeneity, seed abscission and inertia on wind-driven dispersal kernels of tree seeds. J. Ecol. 96, 569–580, http://dx.doi.org/10.1111/j.1365-2745.2008.01368.x.

Bonet, A., 2004. Secondary succession of semi-arid Mediterranean old-fields in south-eastern Spain: insights for conservation and restoration of degraded lands. J. Arid Environ. 56, 213–233, http://dx.doi.org/10.1016/S0140-1963(03)00048-X.

Bruno, J.F., Stachowicz, J.J., Bertness, M.D., 2003. Inclusion of facilitation into ecological theory. Trends Ecol. Evol. 18, 119–125, http://dx.doi.org/10.1016/S0169-5347(02)00045-9.

Bullock, J., Clarke, R., 2000. Long distance seed dispersal by wind: measuring and modelling the tail of the curve. Oecologia 124, 506–521, http://dx.doi.org/10.1007/PL00008876.

Cain, M., Milligan, B., Strand, A., 2000. Long-distance seed dispersal in plant populations. Am. J. Bot. 87, 1217–1227.

Campbell, D.R., Rochefort, L., Lavoie, C., 2003. Determining the immigration potential of plants colonizing disturbed environments: the case of milled peatlands in Quebec. J. Appl. Ecol. 40, 78–91, http://dx.doi.org/10.1046/j.1365-2664.2003.00782.x.

Cano, A., Navia, R., Amezaga, I., Montalvo, J., 2002. Local topoclimate effect on short-term cutslope reclamation success. Ecol. Eng. 18, 489–498, http://dx.doi.org/10.1016/S0925-8574(02)00010-1.

Catalán, G., 1991. Semillas de árboles y arbustos forestales. Ministerio de Agricultura Pesca y Alimentación, Madrid.

Clifford, H.T., 1959. Seed dispersal by motor vehicles. J. Ecol. 47, 311–315.

Collingham, Y.C., Huntley, B., 2000. Impacts of Habitat Fragmentation and Patch Size upon Migration Rates. Ecol. Appl. 10, 131–144, http://dx.doi.org/10.1890/1051-0761(2000)010[0131:IOHFAP]2.0.CO;2.

R Core Team, 2015. R: A Language and Environment for Statistical Computing.

Coulson, C., Spooner, P.G., Lunt, I.D., Watson, S.J., 2013. From the matrix to roadsides and beyond: the role of isolated paddock trees as dispersal points for invasion. Divers. Distrib. 1–123, http://dx.doi.org/10.1111/ddi.12135.

Cuperus, R., Canters, K., Piepers, A., 1996. Ecological compensation of the impacts of a road. Preliminary method for the A50 road link (Eindhoven-Oss, The Netherlands). Ecol. Eng. 7, 327–349, http://dx.doi.org/10.1016/S0925-8574(96)00024-9.

Deckers, B., Becker, P., De Honnay, O., Hermy, M., Muys, B., 2005. Sunken roads as habitats for forest plant species in a dynamic agricultural landscape: effects of age and isolation. J. Biogeogr. 32, 99–109, http://dx.doi.org/10.1111/j.1365-2699.2004.01101.x.

Donath, T., Holzel, N., Otte, A., 2003. The impact of site conditions and seed dispersal on restoration success in alluvial meadows. Appl. Veg. Sci. 6, 13–22, http://dx.doi.org/10.1111/j.1654-109X.2003.tb00560.x.

Fife, D., 2014. fifer: a collection of miscellaneous functions.

Gómez, J.M., García, D., Zamora, R., 2003. Impact of vertebrate acorn- and seedling-predators on a Mediterranean Quercus pyrenaica forest. For. Ecol. Manage. 180, 125–134, http://dx.doi.org/10.1016/S0378-1127(02)00608-4.

Gómez, J.M., 2003. Spatial patterns in long-distance dispersal of Quercus ilex acorns by jays in a heterogeneous landscape. Ecography 26, 573–584, http://dx.doi.org/10.1034/j.1600-0587.2003.03586.x.

Gómez-Aparicio, L., Zamora, R., Gómez, J.M., Hódar, J.A., Castro, J., Baraza, E., 2004. Applying plant facilitation to forest restoration: a meta-analysis of the use of shrubs as nurse plants. Ecol. Appl. 14, 1128–1138, http://dx.doi.org/10.1890/03-5084.

García-Palacios, P., Bowker, M.A., Maestre, F.T., Soliveres, S., Valladares, F., Papadopoulos, J., Escudero, A., 2011. Ecosystem development in roadside grasslands: biotic control, plant-soil interactions, and dispersal limitations. Ecol. Appl. 21, 2806–2821, http://dx.doi.org/10.1890/11-0204.1.

Hartley, M., 2002. Rationale and methods for conserving biodiversity in plantation forests. For. Ecol. Manage. 155, 81–95, http://dx.doi.org/10.1016/S0378-1127(01)00549-7.

Herrera, J., Morales, J., García, D., 2011. Differential effects of fruit availability and habitat cover for frugivore-mediated seed dispersal in a heterogeneous landscape. J. Ecol. 99, 1100–1107, http://dx.doi.org/10.1111/j.1365-2745.2011.01861.x.

Hersperger, A.M., Forman, R.T.T., 2003. Adjacency arrangement effects on plant diversity and composition in woodland patches. Oikos 101, 279–290.

Jacquemyn, H., Butaye, J., Dumortier, M., Hermy, M., Lust, N., 2001. Effects of age and distance on the composition of mixed deciduous forest fragments in an agricultural landscape. J. Veg. Sci. 12, 635–642, http://dx.doi.org/10.2307/3236903.

Jiménez, M.D., Ruíz-Capillas, P., Mola, I., Pérez-Corona, E., Casado, M.A., Balaguer, L., 2013. Soil development at the roadside: a case study of a novel ecosystem. Land Degrad. Dev. 24, 564–574, http://dx.doi.org/10.1002/ldr.1157.

Jordano, P., Godoy, J., 2002. The dynamics of frugivore- generated seed shadows: demographic and genetic effects. In: Levey, D.J., Silva, W., Galetti, M. (Eds.), Seed Dispersal and Frugivory: Ecological, Evolutionary, and Conservation. CABI Publishing, Wallingford, pp. 305–321.

Kluza, D., Griffin, C., Degraaf, R., 2000. Housing developments in rural New England: effects on forest birds. Anim. Conserv. 3, 15–26.

Kurokochi, H., Toyama, K., Hogetsu, T., 2010. Regeneration of robinia pseudoacacia riparian forests after clear-cutting along the chikumagawa river in Japan. Plant Ecol. 210, 31–41, http://dx.doi.org/10.1007/s11258-010-9735-8.

Levey, D., Tewksbury, J., Bolker, B., 2008. Modelling long-distance seed dispersal in heterogeneous landscapes. J. Ecol. 96, 599–608, http://dx.doi.org/10.1111/j.1365-2745.2008.01401.x.

Méndez, M., García, D., Maestre, F.T., Escudero, A., 2008. More ecology is needed to restore mediterranean ecosystems: a reply to valladares and gianoli. Restor. Ecol. 16, 210–216, http://dx.doi.org/10.1111/j.1526-100X.2008.00390.x.

Münzbergová, Z., Herben, T., 2005. Seed, dispersal, microsite, habitat and recruitment limitation: identification of terms and concepts in studies of limitations. Oecologia 145, 1–8, http://dx.doi.org/10.1007/s00442-005-0052-1.

Münzbergová, Z., 2004. Effect of spatial scale on factors limiting species distributions in dry grassland fragments. J. Ecol. 92, 854–867, http://dx.doi.org/10.1023/A:1009770924942.

Magro, S., Jiménez, M.D., Casado, M.A., Mola, I., Arenas, J.M., Martín-Duque, J.F., Vazquez, A., Balaguer, L., 2014. Community ontogeny at the roadside: critical life-cycle events throughout a sequential process of primary colonization. Appl. Veg. Sci. 17, 493–503, http://dx.doi.org/10.1111/avsc.12095.

Malanson, G., Cairns, D., 1997. Effects of dispersal, population delays, and forest fragmentation on tree migration rates. Plant Ecol. 131, 67–79, http://dx.doi.org/10.1023/A:1009770924942.

Mola, I., Jiménez, M.D., López-Jiménez, N., Casado, M.A., Balaguer, L., 2011. Roadside reclamation outside the revegetation season: management options under schedule pressure. Restor. Ecol. 19, 83–92, http://dx.doi.org/10.1111/j.1526-100X.2009.00547.x.

Nathan, R., Horn, H.S., Chave, J., Levin, S.A., 2002. Mechanistic models for tree seed dispersal by wind in dense forests and open landscapes. In: Levey, D.J., Silva, W.R., Galetti, M. (Eds.), Seed Dispersal and Frugivory: Ecology, Evolution and Conservation. CABI Publishing, Wallingford, pp. 69–82.

Nathan, R., 2006. Long-distance dispersal of plants. Science 313 (5788), 786–789, http://dx.doi.org/10.1126/science.1124975.

National Geographic Institute of Spain, 2011. PNOA Plan Nacional de Ortofotografía Aérea [WWW Document]. URL http://www.ign.es/PNOA/.

Olander, L.P., Scatena, F., Silver, W.L., 1998. Impacts of disturbance initiated by road construction in a subtropical cloud forest in the Luquillo Experimental Forest, Puerto Rico. For. Ecol. Manage. 109, 33–49, http://dx.doi.org/10.1016/S0378-1127(98)00261-8.

Pausas, J.G., Bonet, A., Maestre, F.T., Climent, A., 2006. The role of the perch effect on the nucleation process in Mediterranean semi-arid oldfields. Acta Oecol. 29, 346–352, http://dx.doi.org/10.1016/j.actao.2005.12.004.

Pickering, C., Mount, A., 2010. Do tourists disperse weed seed? A global review of unintentional human-mediated terrestrial seed dispersal on clothing, vehicles and horses. J. Sustain. Tour. 18, 239–256, http://dx.doi.org/10.1080/09669580903406613.

Pons, J., Pausas, J.G., 2007. Not only size matters: acorn selection by the European jay (Garrulus glandarius). Acta Oecol. 31, 353–360, http://dx.doi.org/10.1016/j.actao.2007.01.004.

Pounden, E., Greene, D., Quesada, M., 2008. The effect of collisions with vegetation elements on the dispersal of winged and plumed seeds. J. Ecol. 96, 591–598, http://dx.doi.org/10.1111/j.1365-2745.2008.01380.x.

Prach, K., Hobbs, R., 2008. Spontaneous succession versus technical reclamation in the restoration of disturbed sites. Restor. Ecol. 16, 363–366, http://dx.doi.org/10.1111/j.1526-100X.2008.00412.x.

QGIS Development Team, 2013. QGIS Geographic Information System.

Rey Benayas, J.R., Bullock, J.M., Newton, A.C., 2008. Creating woodland islets to reconcile ecological restoration, conservation, and agricultural land use. Front. Ecol. Environ. 6, 329–336, http://dx.doi.org/10.1890/070057.

Sanz-Elorza, M., Dana Sánchez, E., Sobrino Vesperinas, E., 2004. Atlas de las plantas alóctonas invasoras de España. Organismo Autónomo Parques Nacionales, Madrid.

Schurr, F., Steinitz, O., Nathan, R., 2008. Plant fecundity and seed dispersal in spatially heterogeneous environments: models, mechanisms and estimation. J. Ecol. 96, 628–641, http://dx.doi.org/10.1111/j.1365-2745.2008.01371.x.

Singh, A.N., Raghubanshi, A.S., Singh, J.S., 2002. Plantations as a tool for mine spoil restoration. Curr. Sci. 82, 1436–1441.

Siscart, D., Diego, V., Lloret, F., 1999. Acorn ecology. In: Rodà, F., Retana, J., Gracia, C.A., Bellot, J. (Eds.), Ecology of Mediterranean Evergreen Oak Forests. Springer, Berlin, pp. 75–86.

Spooner, P., Smallbone, L., 2009. Effects of road age on the structure of roadside vegetation in south-eastern Australia. Agric. Ecosyst. Environ. 129, 57–64, http://dx.doi.org/10.1016/j.agee.2008.07.008.

Taylor, K., Brummer, T., Taper, M.L., Wing, A., Rew, L.J., 2012. Human-mediated long-distance dispersal: an empirical evaluation of seed dispersal by vehicles. Divers. Distrib. 18, 942–951, http://dx.doi.org/10.1111/j.1472-4642.2012.00926.x.

Tormo, J., Bochet, E., García-fayos, P., 2006. Is seed availability enough to ensure colonization success?An experimental study in road embankments. Ecol. Eng. 26, 224–230, http://dx.doi.org/10.1016/j.ecoleng.2005.10.003.

Tormo, J., Bochet, E., García-Fayos, P., 2009. Restauración y revegetación de taludes de carreteras en ambientes mediterráneos semiáridos: procesos edáficos determinantes para el éxito. Ecosistemas 18, 79–90.

Torre, R., Jiménez, de, Ramírez, M.D., Mola, Á., Casado, I., Balaguer, M.Á., 2015. Use of restoration plantings to enchance bird seed dispersal at the roadside: failures and prospects. J. Environ. Eng. Landscape Manag. 23, 302–311, http://dx.doi.org/10.3846/16486897.2015.1079529.

Turner, M., Gardner, R.H., O'Neill, R.V., 2001. Landscape Ecology in Theory and Practice. Pattern and Processes. Springer, New York, New York, USA.

Verdú, M., García-Fayos, P., 1996. Nucleation processes in a Mediterranean bird-dispersed plant. Funct. Ecol. 10, 275–280, http://dx.doi.org/10.2307/2389853.

Walker, L.R., Velázquez, E., Shiels, A.B., 2009. Applying lessons from ecological succession to the restoration of landslides. Plant Soil 324, 157–168, http://dx.doi.org/10.1007/s11104-008-9864-1.

Wichmann, M.C., Alexander, M.J., Soons, M.B., Galsworthy, S., Dunne, L., Gould, R., Fairfax, C., Niggemann, M., Hails, R.S., Bullock, J.M., 2009. Human-mediated dispersal of seeds over long distances. Proc. Biol. Sci. 276, 523–532, http://dx.doi.org/10.1098/rspb.2008.1131.

With, K., 2002. The landscape ecology of invasive spread. Conserv. Biol. 16, 1192–1203, http://dx.doi.org/10.1046/j.1523-1739.2002.01064.x.

Wydhayagarn, C., Elliott, S., Wangpakapattanawong, P., 2009. Bird communities and seedling recruitment in restoring seasonally dry forest using the framework species method in Northern Thailand. New For. 38, 81–97, http://dx.doi.org/10.1007/s11056-009-9133-z.

Zamora, R., Hódar, J.A., Matías, L., Mendoza, I., 2010. Positive adjacency effects mediated by seed disperser birds in pine plantations. Ecol. Appl. 20, 1053–1060.

Zwaenepoel, A., Roovers, P., Hermy, M., 2006. Motor vehicles as vectors of plant species from road verges in a suburban environment. Basic Appl. Ecol. 7, 83–93, http://dx.doi.org/10.1016/j.baae.2005.04.003.

de Mendiburu, F., 2014. agricolae: Statistical Procedures for Agricultural Research.

de la Riva, E.G., Casado, M.A., Jiménez, M.D., Mola, I., Costa-Tenorio, M., Balaguer, L., 2011. Rates of local colonization and extinction reveal different plant community assembly mechanisms on road verges in central Spain. J. Veg. Sci. 22, 292–302, http://dx.doi.org/10.1111/j.1654-1103.2010.01248.x.

von der Lippe, M., Bullock, J.M., Kowarik, I., Knopp, T., Wichmann, M., 2013. Human-mediated dispersal of seeds by the airflow of vehicles. PLoS One 8, e52733, http://dx.doi.org/10.1371/journal.pone.0052733.

Suplementary Material

The influence of site factors and proximity of adjacent vegetation on tree regeneration into roadslopes

Suplementary results associated with the article: Arenas, J.M. et al. "The influence of site factors and proximity of adjacent vegetation on tree regeneration into roadslopes". Ecological Engineering

Table S1. Relationship between the intrinsic variables of the roadslope and occurrence of individuals of each species. Type of slope (roadcut *vs* embankment), age (new *vs* old), aspect (east *vs* west), lithology (acid *vs* basic), slope and altitude was considered. For the discrete variables the relationship was analyzed with Fisher's exact test, whereas for the continuous variables (i.e. slope and altitude), we used a binomial generalized linear model. The figures correspond with p-values. Bold values indicate significant differences ($p < 0.05$).

Quercus ilex	0.071	**< 0.001**	0.247	0.359	0.456	0.389
Quercus pyrenaica	0.094	**0.004**	0.358	0.544	**< 0.001**	**0.002**
Populus nigra	0.861	0.063	0.179	0.830	**0.048**	0.189
Fraxinus angustifolia	0.322	**0.034**	0.751	0.165	**0.004**	0.070
Ulmus pumila	0.091	0.282	1.000	**0.011**	**0.003**	0.070
Salix spp.	0.212	1.000	1.000	0.635	0.864	0.526

Table S2. Relationship between occurrence of each species on the roadslopes and its

presence at short and medium distances. The relationship has been analyzed by Fisher's

exact test. Bold values indicate significant differences (p < 0.05). All significant

relationships correspond to positive associations.

Occurrence	Occurrence at 0-20 m	Occurrence at 20-150 m
Quercus ile	**< 0.001**	**< 0.001**
Quercus py	**< 0.001**	**< 0.001**
Populus nig	**< 0.001**	**< 0.001**
Fraxinus a	0.129	**< 0.001**
Ulmus pum	1.000	**0.002**
Salix spp.	0.273	**0.001**

Table S3a. Influence of different variables related to the surrounding landscape on species occurrence on the roadslopes. Tree cover and landscape structure were evaluated at three distances from the road. The influence of type of landscape (agricultural *vs* forestry) and landscape structure (without trees, scattered trees, scattered woods or forest) on the occurrence of each species in the roadslopes was tested with the use of the Fisher exact test. The relationship between occurrence on the roadslope and tree cover at short (0-20 m), medium (20-150 m) and long distances (150-500 m) was tested with the binomial generalized linear model. The figures correspond with p-values. Bold values indicate significant differences ($p < 0.05$).

	Type of landscape	Tree cover 0-20	Tree cover 20-150	Tree cover 150-500	Structure 0-20	Structure 20-150	Structure 150-500
Quercus ilex	**0.004**	**0.014**	**0.000**	**0.000**	**0.018**	0.108	**0.000**
Quercus pyrenaica	**0.000**	**0.000**	**0.000**	**0.000**	**0.022**	**0.000**	**0.000**
Populus nigra	0.076	0.373	0.172	0.078	0.419	0.486	0.137
Fraxinus angustifolia	**0.015**	0.955	0.955	0.622	0.30	0.085	0.527
Ulmus pumila	**0.015**	0.95	0.955	0.566	0.307	0.254	0.527
Salix spp.	0.748	0.271	0.354	0.744	0.926	0.368	0.348

Table S3b. Post-hoc comparison within the four categories of landscape structure. Only the species showing significant relationships between landscape structure and occurrence on the roadslopes (see Table S3a) were considered.

		Quercus ilex	*Quercus pyrenaica*
	Without trees	b	b
0-20 m	Scattered trees	a	a
	Scattered woods	ab	ab
	Forest	ab	ab
			Quercus pyrenaica
	Without trees		c
20-150 m	Scattered trees	-	b
	Scattered woods		b
	Forest		a
		Quercus ilex	*Quercus pyrenaica*
	Without trees	b	b
150-500 m	Scattered trees	b	b
	Scattered woods	b	b
	Forest	a	a

—

Capítulo 4
Roadsides:
An opportunity
for biodiversity
conservation

—

J.M. Arenas, A. Escudero, I. Mola, M.A. Casado.

-

Articulo enviado por primera vez el 11 de Octubre de 2016, reenviado tras modificaciones el 7 de Marzo de 2017 y actualmente con decision de Mayor Revision (5 de Abril de 2017). La mayoría de cambios propuestos han sido ya recogidas en el presente capítulo de la tesis.
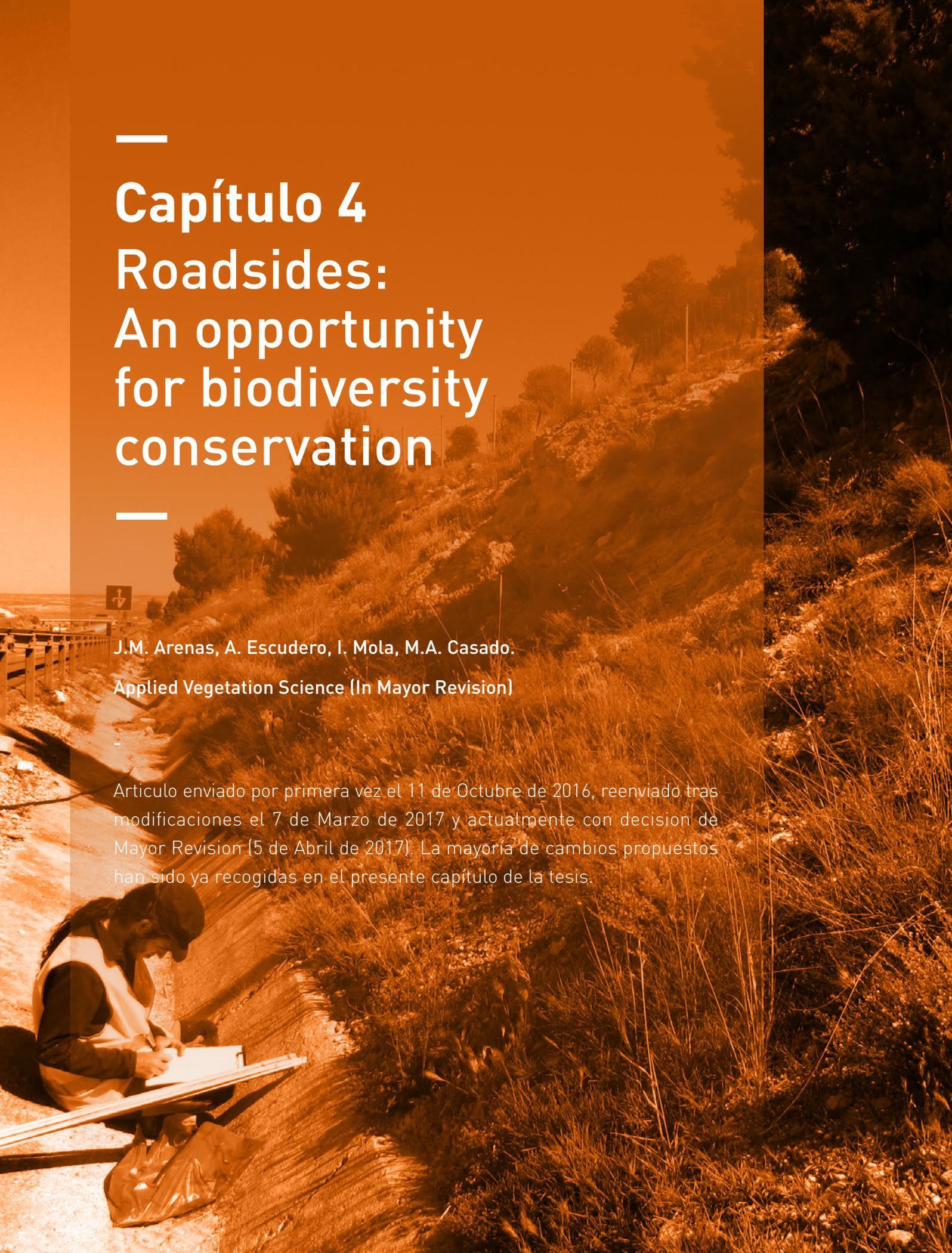
Roadsides: An opportunity for biodiversity conservation

Juan M. Arenas[1]*, Adrián Escudero[2], Ignacio Mola[3], Miguel A. Casado[1].

Arenas, J. M. (jmarenas@ucm.es) [1]*
Escudero, A. (adrian.escudero@urjc.es) [2]
Mola, I. (imola@ohl.es) [3]
Casado, M. A. (mcasado@ucm.es) [1]

1 Departamento de Ecología, Universidad Complutense de Madrid, 28040 Madrid, Spain
2 Unidad de Biodiversidad y Conservación, Departamento de Biología y Geología, Universidad Rey Juan Carlos, Móstoles, 28933 Madrid, Spain
3 Research, Development and Innovation (R&D) Service, Obrascón Huarte Lain, S.A. (OHL), 28046 Madrid, Spain

* Author for correspondence:
  jmarenas@ucm.es

. . . .

ABSTRACT

Questions

How do roadsides interact with patches of natural vegetation in shaping perennial plant communities in fragmented agricultural areas? Are the observed differences due to the type of roadside (i.e., roadcuts, embankments or road verges) or are there other factors driving community structure and composition?

Location

Stretch of motorway A3 and its surrounding area, in central Spain.

Methods

We analysed the variation in perennial plant species composition and diversity among 92 plots (400 m^2). The plots were located in five different environmental scenarios, three of them in a fragmented landscape (patches of natural vegetation, embankments, and roadcuts) and two in an unfragmented landscape (natural vegetation and road verges). In each plot, the cover of each perennial plant species and eight soil variables were assessed. We used phi coefficient of correlation to determine the scenario preferences of each species, Kruskal-Wallis tests to compare the soil variables between landscape scenarios and eight descriptive variables of the community, and RDA and partial RDA analysis to evaluate the relative importance of the type of environmental scenario on the floristic community.

Results

We identified 130 species, with only 16 species never appearing on roadsides. Perennial total cover, species richness, inverse Simpson's index and number of protected species showed no significant differences between the five scenarios considered. In contrast, the number of nutrient-demanding species and restricted-range diversity showed lower values in natural vegetation plots. Soil variables and the type of scenario together explained 28.5% of the species composition variation. Of this percentage, 6.8% was explained by soil variables, 12.1% by the type of scenario and 10.0% of the variation was shared between the two datasets.

Conclusions

Our results show that almost all perennial species occurring in natural vegetation patches were also able to reach and settle in the roadsides. However, soil conditions and other specific roadside variables generate different plant communities. In spite of the differences found between the perennial plant community of roadsides and their surrounding area, roadsides are excellent reservoirs of biodiversity.

INTRODUCTION

Transport infrastructure is generally perceived as having negative impacts on ecosystems (Forman & Alexander 1998). Habitat fragmentation, mortality from road construction and collision with vehicles, modification of animal behaviour, alterations of the physical and chemical environment and the spread of exotic species, among other impacts, have been described (for a review, see Trombulak & Frissell 2000). However, linear infrastructures may provide habitats that strengthen ecosystem services, especially those that are particularly weak in humanized landscapes (Millennium Ecosystem Assessment 2005). Thus, minimizing these adverse effects or placing them in a broader ecological context, for instance considering these emergent positive opportunities, may help to draw a more precise picture of the impact of linear transport infrastructures in the territory.

In recent decades, intensification of agricultural activities has triggered the loss of critical landscape elements for diversity (e.g. fallow land, borders, marginal lands, etc.), which has led to a decrease in biodiversity and ecosystem services (Benton et al. 2003; Karp et al. 2012). Within these intensive modified farming areas, road margins can be a management priority and an opportunity for biodiversity conservation, increasing landscape heterogeneity and providing refuge for certain species (Tikka et al. 2000; Helden & Leather 2004; Spooner & Smallbone 2009; Zeng et al. 2011). In this context infrastructure margins can play an important role in ecosystem dynamics, since they can generate ecological flows to and from these areas reinforcing the connectivity among remnants (Lugo & Gucinski 2000). For instance, understanding the role of linear infrastructures and how they interact with a fragmented agricultural landscape is critical to determining their net effect on diversity from a global perspective. More specifically, determining whether linear infrastructures can serve as an opportunity for conservation management should be a priority, especially in high-income countries.

The role of roadsides in acting as reservoirs of biodiversity can be expressed differently for each species, biological group and community type (Auffret & Cousins 2013). Here we focused our study on perennial vegetation because it contains a number of advantages over other biological guilds, such as annual plants. First, perennials are more persistent over time, which makes their population dynamics less dependent on weather conditions in a given year (Polis et al. 1997;

Gutiérrez et al. 2000; Caballero et al. 2008). Second, biotic interactions (e.g., facilitation, competition) between species can be extended over years, allowing more structured and stable communities. Moreover, perennial vegetation, such as woody plants and tussock grasses, are well-known as facilitators for the establishment of other species by improving abiotic conditions, such as enhanced soil nutrients, water availability and microclimatic heterogeneity, especially in harsh environments (Jones et al. 1994; Perelman et al. 2003; Gómez-Aparicio et al. 2004; Wilby & Shachak 2004; Luzuriaga et al. 2012).

The aim of this study is to analyse the composition and structure of communities of perennial plants on the roadsides of a highway in central Spain, comparing them with those of their surrounding areas at a landscape scale. The territory dissected by this highway is mainly agricultural with small patches of natural vegetation. These patches are a mosaic of gypsum (calcium sulfate) soil habitats, which are characteristic of arid and semi-arid environments and are widespread with over 100 million ha worldwide (Verheye & Boyadgiev, 1997). Gypsophiles are dependent on the special physical and chemical features of this type of soil (Escudero et al. 2014). Gypsum plant communities shelter an unusual flora very rich in narrow endemic and endangered species. For this reason, it is critical to determine if these roadside margins can contribute to conserving some of the most remarkable biodiversity hotspots in terrestrial European ecosystems (see European Directive for Conservation of Habitats and Wild Fauna and Flora; Directive 92/43/CEE, 1992). Unfortunately, the synergic effect of global change drivers operating simultaneously in the territory, such as climate warming, landscape fragmentation and human-driven degradation, are positioning these habitats at a critical point (see Escudero et al. 2014). Therefore, knowing if these roadsides can alleviate this pressure and how they can strengthen biodiversity conservation in gypsum habitats is of special interest, particularly

to developing proper ecological restoration and conservation measures.

Specifically, we try to answer the following question: How do roadsides interact with patches of natural vegetation in shaping perennial plant communities in fragmented agricultural landscapes? We compare natural vegetation and road margins at the species and community levels, including structural, functional and species conservation indices. We also examine whether the observed differences are caused by the type of roadside (roadcuts, embankments or road verges), given their different soil characteristics generated by road construction. By addressing these questions, we seek to contribute to understanding whether adequate interventions in roadsides can promote their ability to generate or encourage certain ecosystem services. Specifically, we focus on the creation of refuges for species and plant communities of interest, and its implications for biodiversity conservarion.

MATERIAL AND METHODS

Study area

This study was conducted in the surroundings of motorway A3, on the regional border between Madrid and Castilla-La Mancha autonomous regions, in central Spain (40º9'28''N, 3º15'23''W and 40º2'5''N, 3º2'40''W). This road has been operative as a motorway for more than thirty years. The selected stretch is 15 km and passes a massive gypsum outcrop dissecting two different types of landscape. In most of the study area, the highway passes through an extensive landscape of cereal agriculture where small patches of remnant natural vegetation remain (Fig. 1). In contrast, at its northern end, there are large well-preserved areas of natural vegetation. This territory has a homogeneous semi-arid Mediterranean climate with a mean annual rainfall of 525 mm, and average annual temperatures of 13.7 ºC (from the nearest weather station in Belinchón,
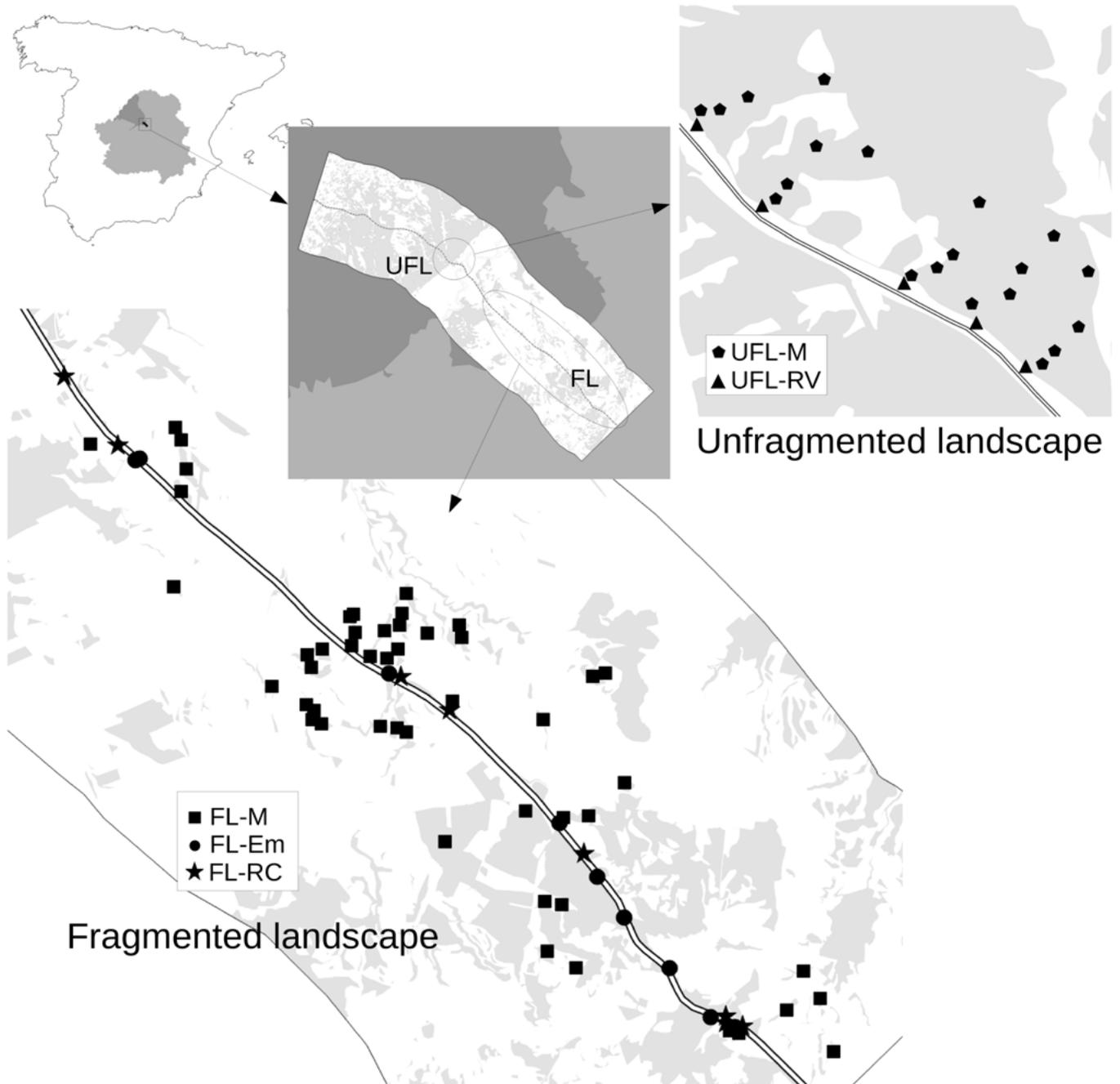
Figure 1. Study area. Location of the 92 sampling plots along a 15 km x 6 km band on the A-3 motorway in Madrid-Valencia (central Spain). On the map of Spain, the gray areas represent Madrid (dark gray) and Castilla-La Mancha (gray) autonomous regions. On the Fragmented landscape (FL) map and Unframented landscape (UFL) map, the light gray colour corresponds to areas of natural vegetation. UFL-M: Natural matrix in unfragmented landscape, UFL-Rv: Road verges in unfragmented landscape, FL-M: Natural matrix in fragmented landscape, Em: Embankments in fragmented landscape, Rc: Roadcuts in fragmented landscape.

Cuenca, 40º2'54''N, 3º3'29''W). Precipitation distribution shows major rainfall periods in early spring and late autumn and extremely intense summer droughts.

Sampling plots

We selected 92 sampling plots (400 m^2 each) embedded in the two landscape types: the agricultural

landscape located on both sides of the highway in a rectangular surface area of 13 km long and 3 km wide (hereafter Fragmented Landscape or FL) and the area of continuous natural vegetation in a rectangular surface area of 2.5 km long and 0.4 km wide (hereafter Unfragmented Landscape or UFL) (Fig. 1). In the Fragmented Landscape, we randomly selected 50 fragments of natural vegetation and placed a plot in each of them (natural matrix in fragmented landscape or FL-M). Fragment area ranged from 0.05 to 102 ha. In addition, in this region we randomly selected 8 embankments (FL-Em) and 9 roadcuts (FL-Rc), placing a plot in each of them. A sufficient number of years had passed since the construction of all roadslopes to maintain a well-developed perennial plant cover. These two types of roadslopes have very different origins and environmental characteristics. Roadcuts are constructed by excavation, generating areas of bare soil and exposed bedrock. Embankments are constructed by heaping and compacting materials and eventually applying topsoil treatments (Tormo et al. 2009). In the Unfragmented Landscape, five transects perpendicular to the road and 400 m long were selected. In each transect the first plot was always adjacent to the road and corresponded to a relatively flat or low slope road verge (UFL-Rv; 5 plots). Twenty plots were sampled at different distances from the highway: 50, 100, 200 and 400 m (natural matrix in Unfragmented landscape or UFL-M). In summary, five gypsum habitat scenarios were considered: FL-M, FL-Em, FL-Rc, UFL-M and UFL-Rv.

Vegetation sampling

We tried to select areas with a northern-facing orientation to minimize bias in structure and composition due to insolation. Inside each of the 92 plots, five 2.4 x 2.4 m quadrats were established. In FL-M, UFL-M and UFL-Rv four quadrats were distributed at the corners of the plot and the fifth at the centre. In FL-Em and FL-Rc, the five sampling quadrats were established linearly in the centre of the plots to reduce the impact of roadslope

management practices, which usually occur near the road or in the upper flat areas. Total perennial plant cover was visually estimated for each quadrat and the average of the five quadrats per plot was calculated. The percentage cover of each perennial plant species was also visually estimated for each quadrat. This plant sampling was complemented by random survey walks, taking note of those species that had not appeared in the five quadrats. Finally, the percentage cover of each plant was calculated as the average of the 5 quadrats, adding 0.1% to the species identified only in random walk surveys. Cover species was recorded in the spring, during the phenological peak of the community.

Plant species were characterized considering different ecological features (i.e., nutrient-demanding species and gypsum tolerance) and biogeographical information (Iberian endemicity) as well as their conservation status (protected species). Nutrient-demanding species (with two categories: nutrient-demanding and non-nutrient-demanding species; *sensu* Castroviejo 1986-2016; Rivas-Martínez et al. 2002) represent the species' capacity to grow in soils with high nutrient availability (indicative of disturbance and human-driven alterations) or low nutrient availability, respectively. The gypsum tolerance of each species was classified into one of three classes: plants that are rare on gypsum soils (1: waifs), plants that grow both on and off gypsum soils (2: gypsovags) and plants growing exclusively on gypsum soils (3: gypsophiles) (Castroviejo 1986-2016; Mota et al. 2009). Iberian endemicity of the species was assigned according to Aedo et al. (2013). Species listed in the National Catalogue of Endangered Species (MMAMM 2011) or in the Madrid or Castilla-La Mancha regional Catalogues of Endangered Species (CAM 1992; DOCM 1998, respectively) were considered as species demanding protection. Each species was considered protected or unprotected, regardless of the level of protection.

In summary, for each plot we assessed total cover, species richness, and the number of protected, endemic and nutrient-demanding species. We also calculated a

gypsophily index as the community weighted mean for the average gypsum tolerance level of species listed in each plot. We calculated the inverse Simpson's index and the restricted-range diversity. The restricted-range diversity indicates the floral uniqueness of a site in relation to other sites. To derive this index for each plot, the inverse numbers of sites in which each species occurs are summed, expressing this sum as a percentage of the total scores for all the species in the data set (Kershaw et al. 1994).

Soil sampling

In each plot three soil cores (5 cm in diameter and 10 cm deep) were collected in bare zones and three soil cores, excluding the aboveground biomass and litter, were collected under shrub canopy. These samples were taken in August, when the soil was dry. Soil samples were air dried for one month and sieved through a 2 mm mesh. Eight soil variables were evaluated. Total organic carbon (C), total nitrogen (N), total phosphorus (P), and potassium (K) constitute "slow variables" (sensu Reynolds et al. 2007) and are related to the primary productivity and soil resource stocks (see Maestre et al. 2012). In addition, two soil enzyme activities related to carbon dynamics (ß-glucosidase) and phosphorus (phosphatase) cycles were measured as an estimate of "rapid variables" (Reynolds et al. 2007), which are tightly dependent on the current soil microbial diversity and functionality. Finally, electrical conductivity and pH were also measured. The laboratory techniques used to determine each soil parameter are explained in Appendix S1. Taking into account the perennial plant cover and bare ground surface of each plot, we calculated a weighted averaged mean value per soil variable considering the samples taken in bare zones and under shrub canopy.

Data analyses

In a first step, we determined the preference of each species for the five environmental scenarios: FL-M,

FL-Em, FL-Rc, UFL-M, UFL-Rv. We only considered species that appeared in more than 20% of the plots in at least one of the five scenarios. The association of these species with the five scenarios was assessed by using the phi coefficient of correlation for groups of unequal size (sensu De Cáceres and Legendre 2009) with the 'indicspecies' R package (De Cáceres and Legendre 2009; R Core Team, 2015). Statistical significance of phi values was assessed by 999 permutations at P < 0.05.

The percentage of perennial total cover, species richness, inverse Simpson's index, the number of protected, endemic and nutrient demanding species, the restricted-range diversity and gypsophily index per plot were compared among the five types of scenarios. These comparisons were carried out with the Kruskal Wallis test and, when this test was significant, using the Conover-Iman test for post-hoc analysis. Analyses were performed using the "kruskal()" function in the "agricolae" R package (de Mendiburu 2014). The Bonferroni correction was used to adjust p values for multiple comparisons. The eight soil variables were compared in the same way.

The relative importance of the type of environmental scenario on the floristic matrix was evaluated using redundancy analysis (RDA). Again, we only considered species that appeared in more than 20% of the plots in at least one of the five scenarios. Because Euclidean distance (used in RDA) is inappropriate for raw species abundance data involving many zero values, the species matrix was transformed using Hellinger standardization (Legendre & Gallagher 2001). RDA was performed using the "rda()" function in the "vegan" R package (Oksanen et al. 2015). In addition, in order to know if there were differences among scenarios, we transformed this multinomial variable into five dummy variables. We then performed five RDAs excluding one scenario in each RDA and comparing the significance with the four scenarios included. The significance ("Type III" ANOVA) of each scenario in the five RDA's was analysed using permutation tests with 999 randomizations using

the "vegan" R package. To know if the soil variables determined the structure of plant communities, the eight soil variables were fitted to the RDA and their significance was tested using the "envfit()" function in the "vegan" R package.

To establish which fractions of variation explained by the type of scenario were due to soil variables instead of genuine variation among scenarios, a variation partitioning with RDA was performed using the "varpart()" function in the "vegan" R package. For these analyses, we excluded the non-significant variables previously detected by a forward selection with "step()" function in the "vegan" R package (Oksanen et al. 2015). Taking into account the forward selection, two soil variables (pH and Organic Carbon) were excluded. Finally, a partial RDA was tested. This partial RDA determines the relative importance of the type of environmental scenario after removing the effect of the soil data matrix. We used the "rda(~ conditions(variables removed) +,)" function in the "vegan" R package. Again, in the same way as for RDA, the differences between all pairs of scenarios were tested in five partial RDAs. Moreover, to graphically show the vegetation response to different environmental scenarios, we plotted both the RDA and the partial RDA.

Finally, the eight descriptive variables of the community (i.e., perennial total cover, species richness, inverse Simpson's index, restricted-range diversity, gypsophily index, number of nutrient-demanding species, number of protected species and number of endemic species) were fitted to RDA and partial RDA and were included in the biplots using the "vegan" R package.

RESULTS

The total number of perennial species found in this study was 130. Of them, 77 were found in more than 20% of the plots in at least one of the 5 scenarios. These species were used to analyse their preferences among scenarios and 46 showed significant differences (phi correlation index, $p < 0.05$; see Electronic Appendix S2). Twenty-two species (48%) had a preference for roadsides (embankments, roadcuts and road verges), of which eight corresponded to embankments. In contrast, only 11 species showed a preference for natural vegetation areas, five of them in patches of fragmented landscape and six in both types of landscapes (see Electronic Appendix S2). Only three species (*Ginandriris* type, *Dipcadi serotinum* and *Gladiolus communis*) never appeared on roadsides, while 13 roadside species were never identified in the natural vegetation. The 53 less frequent species that were not tested showed very similar distribution patterns to that of the most frequent species. Twenty-one species occurred only in roadsides, of which nine were exclusive to embankments. In contrast, 13 species were exclusive to natural vegetation areas, 10 of which were exclusive to remnants of fragmented landscape.

Perennial total cover, species richness, inverse Simpson's index and number of protected species showed no significant differences between the five scenarios considered (Fig. 2). Some variables differentiated both matrix scenarios. This was the case for the number of endemic species (Fig. 2e) and the so-called gypsophily index (Fig. 2g), with higher values in unfragmented than in fragmented landscapes, and the number of nutrient-demanding species (Fig. 2f) with lower values in unfragmented landscapes. The number of nutrient-demanding species was always significantly lower in natural vegetation plots (FL-M and UFL-M) than in embankments or road verges (Fig. 2f). Similarly, restricted-range diversity was also lower in natural vegetation plots compared to embankments (Fig. 2h). Finally, the gypsophily index was higher in natural vegetation plots compared to roadcuts.

Among the soil variables, only phosphorus showed no significant differences between the five scenarios (Fig. 3). Comparing the two types of landscapes (Fragmented and Unfragmented) β-glucosidase, phosphatase and
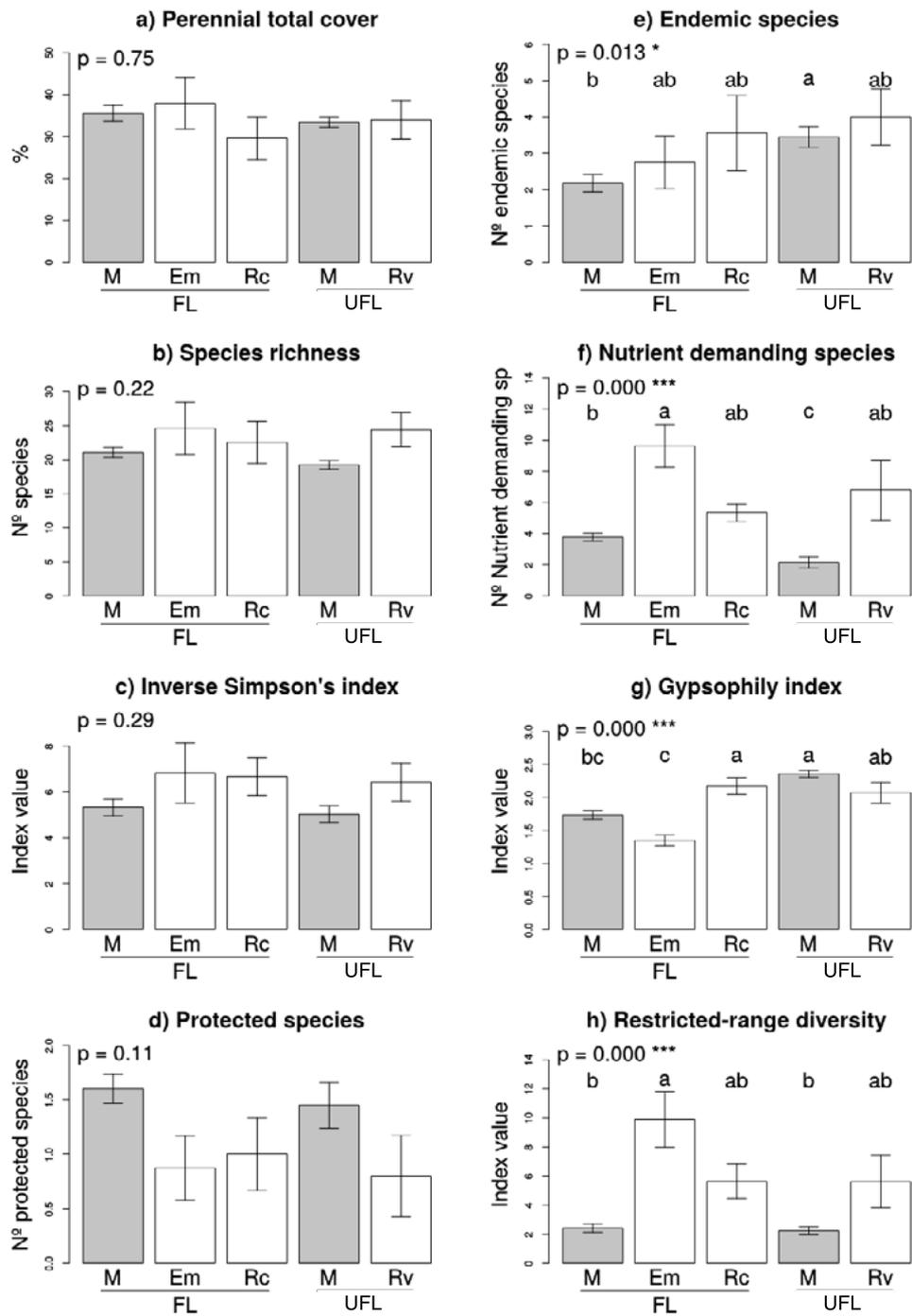
Figure 2. Average values (and S.E.) for eight descriptive variables of the perennial plant community according to type of scenario. FL: Fragmented landscape, UFL: Unfragmented landscape, M: Natural matrix, Em: Embankments, Rc: Roadcuts, Rv: Road verges. For each graph the significance value of the Kruskal-Wallis test is given. Different letters indicate significant differences (Conover–Iman test for post hoc comparisons, p<0.05) among the scenarios.

K reached higher values in the fragmented landscape while electrical conductivity was higher in the unfragmented one. In the unfragmented landscape, no edaphic variables differentiated the matrix from road verge plots, while in the fragmented one FL-M showed large differences with FL-Rc and especially with FL-Em.
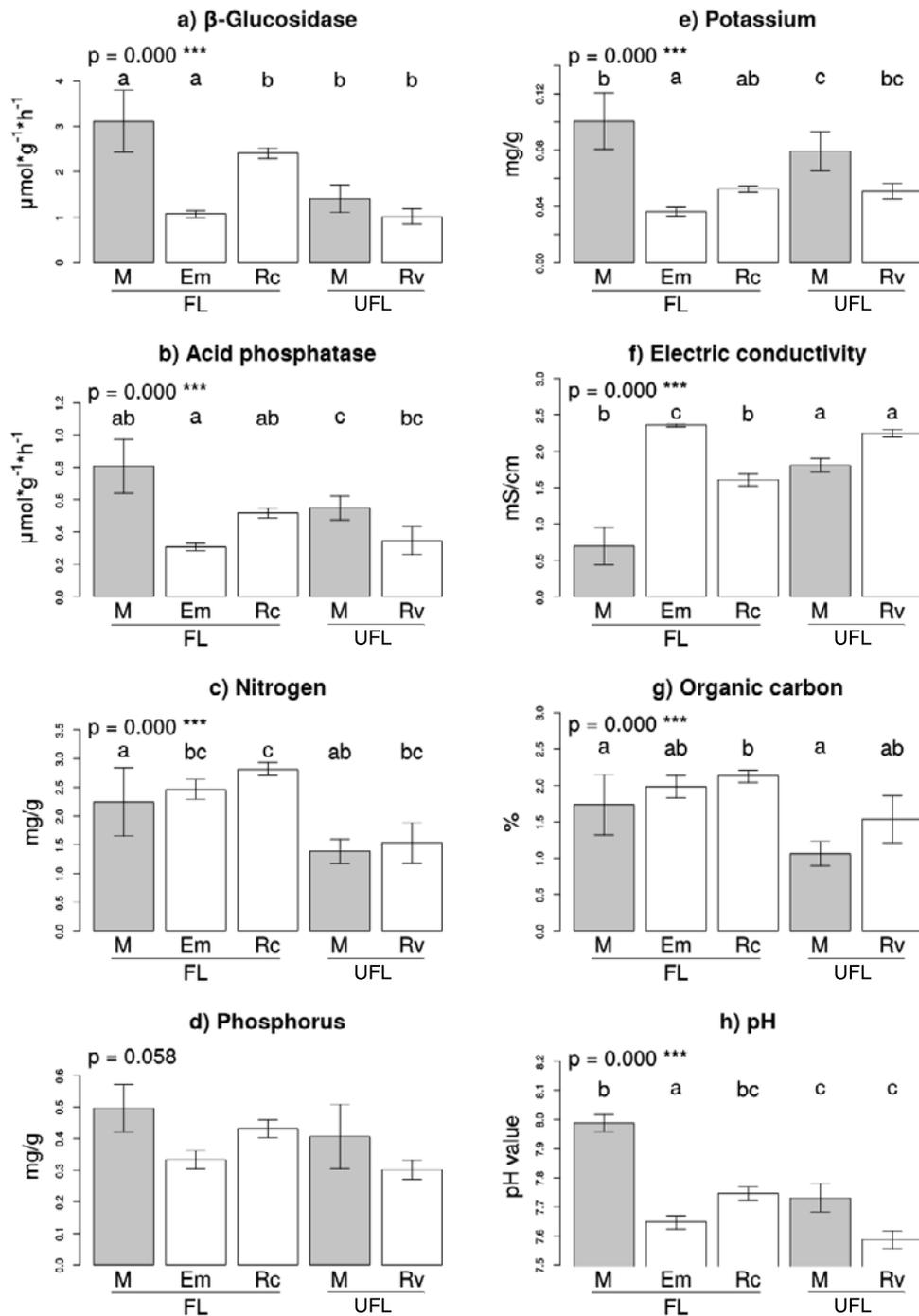
Figure 3. Average values (and S.E.) for the soil variables per environmental scenario. FL: Fragmented landscape, UFL: Unfragmented landscape, M: Natural matrix, Em: Embankments, Rc: Roadcuts, Rv: Road verges. For each graph the significance value of the corresponding Kruskal-Wallis test is given. Different letters indicate significant differences (Conover–Iman test for post hoc comparisons, $p < 0.05$) among the scenarios.

Compared to FL-Rc, FL-M maintained higher values of β-glucosidase, N and organic C, whereas in comparison with FL-Em the greater differences were associated with N and electrical conductivity (higher in FL-M), as well as in K and pH (higher in FL-Em). Finally, among the roadsides, both roadcuts and road verges were very similar while embankments were characterized by their high values of β-glucosidase, phosphatase and pH.

57

The five environmental scenarios significantly explained 25.5% of the variance in the RDA analysis, with a clear floristic separation between the scenarios (Fig. 4a). Permutation tests for the five RDAs with the scenarios as dummy variables showed that all pairs of scenarios, except UFL-M *vs* UFL-Rv, were significantly different. The first axis differentiated the plots from the FL-M scenario (negative coordinates, characterized mainly by *Poa bulbosa*, *Plantago albicans*, *Allium sphaerocephalon*, *Astragalus incanus* and *Thapsia villosa*) from the plots of the other four scenarios (positive coordinates, associated with *Thymus zygis*, *Dactylis glomerata*, *Macrochloa tenacissima*, *Sedum gipsicola* and *Gypsophila struthium*). The second axis separated the unfragmented landscape plots (UFL-M and UFL-Rv) in its most positive values (*Thymus zygis*, *Lepidium subulatum*, *Sedum Gipsicola* and *Centaurea hyssopifolia* showed the higher positive values) from the

FL-Rc and FL-Em plots on the negative edge (*Dactylis glomerata*, *Plantago albicans*, *Helichrysum stoechas*, *Centaurea aspera* and *Marrubium vulgare* as species with the highest negative values). In fitting our target community variables to the RDA, almost all descriptive variables (inverse Simpson's index, restricted-range diversity, gypsophily index, number of nutrient-demanding species, number of protected species and number of endemic species) were significant (Fig. 4a and Electronic Appendix S3). All soil variables also significantly fitted to the first two axes of the RDA (Electronic Appendix S3), demonstrating the importance of soil variables for structuring the plant community.

Variance partitioning results showed that soil and the type of scenario together explained 28.5% of the floristic variation with a shared variation between the two datasets of 10.0%. Soil data explained 6.8% of the floristic variation not explained by the environmental
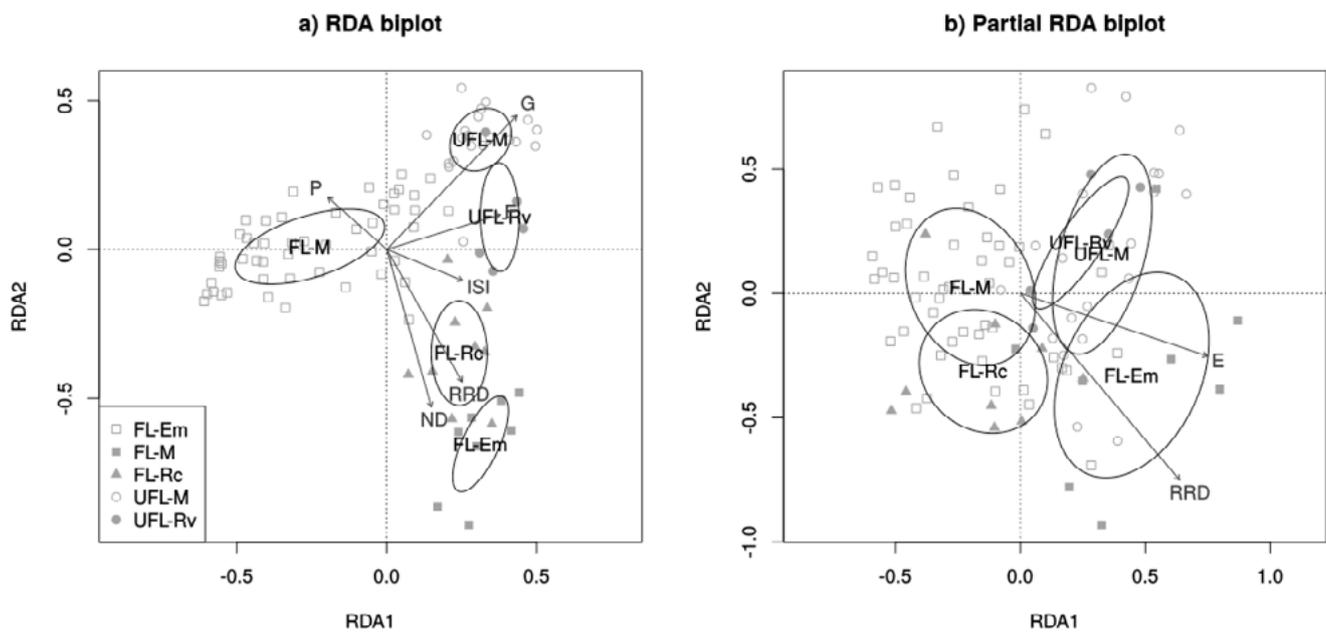
Figure 4. a) RDA using type of scenario as a constraining variable. b) Partial RDA using scenario as a constraining variable, in which the variation attributable to the soil dataset was removed before adjusting the model. Type of scenario codes: FL-M = Natural matrix in fragmented landscape, FL-Em = Embankments in fragmented landscape, FL-Rc = Roadcut in fragmented landscape, UFL-M = Natural matrix in unfragmented landscape, UFL-Rv = Road verges in unfragmented landscape. Ellipses describe standard deviation for each type of scenario. Arrows represent correlations among descriptive variables and biplot axes. Only variables with a significant effect (*P* < 0.05) are shown (Appendix S3 and S4). Descriptive variable codes: P = Number of protected species, E = Number of endemic species, ND = Number of nutrient-demanding species, G = gypsophily index, ISI = Inverse Simpson's index, RRD = Restricted-range diversity.

scenarios. The type of scenario, after removing the variation caused by soil variables, explained 12.1% of the floristic variation, with all of them significantly different from each other. However, this partial RDA biplot (Fig. 4b) showed that the separation between types of scenarios was not as patent as in the previous RDA without partialling out the soil variation (Fig. 4a compared to. 4b). Finally, two of the eight fitted descriptive variables (restricted-range diversity, and number of endemic species) were still significant to partial RDA (Figure 4b and Electronic Appendix S4).

DISCUSSION

Our results indicate that, beyond the known benefits of vegetation as stabilizing roadslopes (Andrés & Jorba 2000; Cerdà 2007), roadsides (road verges, roadcuts and embankments) can host perennial plant communities that are well-defined but slightly differentiated from the vegetation of natural environments. These novel, emergent and human-induced habitats can contribute to the conservation of biodiversity at a regional scale, with many structural and compositional similarities but also major discrepancies from the natural vegetation scenarios. Our results highlight the ability of roadsides to host a diverse and representative flora of the regional species pool, which supports their importance as refuges and reservoirs of biodiversity.

Overall vegetation patterns

Some authors have found higher values of species richness in roadsides compared to surrounding areas (Forman & Alexander 1998; Tikka et al. 2000; Zeng et al. 2011). However, our results do not detect significant differences in vegetation cover, species richness or inverse Simpson's index between the five different types of scenarios considered, although the roadsides showed a very wide range of intra-scenario variation. This variation may be related to different soil conditions (also with a wide range of variation, Fig. 3), to differences

in age (Spooner & Smallbone 2009; Arenas et al. 2015), and to other inherent characteristics of each roadside (e.g. size, common management practices, surrounding matrix).

Despite these similarities in plant cover and diversity, our results indicate that plant communities in roadsides are different from those found in the natural surrounding areas (see also Tikka et al. 2000; Zeng et al. 2011). RDA analysis showed that each ecological scenario maintains significantly different vegetation types. These differences, at a fine scale, may be due to factors associated with seed dispersal and propagule availability or microsite differences or both (Münzbergová & Herben 2005). The presence of most species in the five scenarios contradicts a limitation of seed availability. In contrast, soil variables differ both between the different landscapes and among the scenarios, which, at least partially, indicates that the microsite differences may be a determining factor in the differences in the perennial community. Compared to fragmented landscapes, large areas of natural vegetation show differences in the species they harbour (higher gypsophily index and the number of endemic species, low nutrient-demanding species), which are possibly related to their particular soil features and land use history. In the case of roadsides, it is known that soil characteristics are key in the composition of their plant communities (Mola et al. 2011; Jiménez et al. 2013), and probably become more important in gypsum ecosystems, since gypsum vegetation is very dependent on soil properties (Escudero et al. 2014). Edaphic differences between different roadsides with respect to areas of natural vegetation have been explained by the constructive differences among different types of roadsides (Jiménez et al. 2013). In road verges (UFL-Rv), the soil changes associated with the construction of the road were not very strong. In fact, none of the soil variables studied showed differences between these road verges and their surrounding areas (UFL-M). As a consequence, the vegetation of road verges (UFL-

Rv) showed no major differences in relation to the vegetation of the nearest natural areas (UFL-M). In contrast, the construction of roadslopes (roadcuts and embankments) implies more intense disturbance. On the one hand, the exposed bedrock of roadcuts results in soils that are very similar to those of gypsum habitats (Escudero et al. 2014). Thus, our finding of no differences in some soil characteristics between roadcuts and their natural surrounding areas, but with fewer nutrients (nitrogen and organic carbon), seems reasonable. This nutrient limitation in roadcuts could be critical to generating differences in realized assemblages (Mola et al. 2011). On the other hand, embankments, due to their constructive characteristics, have physicochemical features very different from the rest of the habitat scenarios, including difference in some measured variables such as a higher pH and concentration of potassium, and less electrical conductivity and N. These large edaphic differences could be primarily responsible for the floristic differences associated with embankments. However, variance partitioning and partial RDA analysis showed that soil variables only explain a small part (6.8%) of the floristic variability. This reinforces the idea that many of the differences between scenarios are dependent on soil variables, but not all.

Surprisingly, and in spite of the importance of soil variations, other uncontrolled characteristics may also be relevant in the definition of our plant communities, and particularly in maintaining the differences in plant communities among the different sampling scenarios. Along these lines, both variance partitioning and partial RDA analysis (after removing soil variables) showed that part of the floristic variability depended on the type of scenario, but not on the analysed soil variables. The differences found in plant communities may be related to the particular characteristics and land use history of each scenario, especially the differences between landscape types (UFL *vs* FL) and the high similarity between the matrix and road verges within the

unfragmented landscape. In addition, our results show that plant communities of roadcuts and embankments are similar (RDA, Fig. 4), even though their soil variables are very different. This is due to common characteristics of roadslopes, regardless of the type of roadslope and their large constructive and edaphic differences.

The role of roadsides as refuges and reservoirs of biodiversity

Of all the species analysed, only three bulbous plants (*Dipcadi serotinum*, *Ginandriris* type and *Gladiolus communis*) were abundant and exclusive to natural vegetation. In addition, most of the species in which we detected a clear preference are exclusive to roadsides, especially in embankment plots. These results indicate that most of the entire regional pool of species was able to reach and settle on roadsides. Therefore, the roadsides not only host the majority of the species of the surrounding area, but also incorporate a large number of species adapted to the special environmental conditions of roadsides. This lends them an important role as a reservoir of plants at a regional scale. At least in a very humanized landscape like the one studied, this value as a reservoir of species largely mitigates the loss of both species richness and beta-diversity associated with intensive agriculture (Benton et al. 2003; Strijker 2005; Karp et al. 2012).

This remarkable diversity is reinforced by the fact that these road margins are important for rare species at a regional scale as shown by the restricted-range diversity. In this study, the restricted-range diversity was highest in embankments, followed by the other two roadside types. In addition, our results suggest that the floral uniqueness of a site is not, or not only, associated with soil differences, because this variable is closely associated with the centroid of the embankment plots once the soil variability was partialled out. The high restricted-range diversity in roadsides indicates that these sites serve as a refuge for certain rare species, not usually present in the surrounding areas,

at a regional scale (see also Tikka et al. 2000). These rare species may be typical of habitats not considered in this study, such as crop borders or fallow lands, which are disappearing because of intensive farming (Strijker 2005). Therefore, roadsides may be helping to maintain this flora at a regional scale (see also Spooner & Smallbone 2009).

Roadsides also have the capacity to host important species from a conservation the point of view, as has been highlighted by other authors (Parr & Way 1988; Breckwoldt 1990; Melman & Verkaar 1991). Our results show that roadsides have a similar number of interesting species for conservation (protected and endemic species) as the surrounding areas of natural vegetation. It is also noteworthy that *Limonium dichotomum* and *Limonium toletanum*, which are species of "special concern" in the Regional Catalogue of Endangered Species of Castilla-La Mancha (DOCM, 1998), are mostly in roadcuts and embankments.

Conclusions and recommendations for practitioners and administration

The European Union places special emphasis on the "Green Infrastructures" concept seeking to promote connectivity between regions to mitigate the current loss of biodiversity (European Commission 2010). Our results demonstrate that roadsides can be excellent reservoirs of biodiversity. Therefore, the road network, given its linear geometry and high density in developed countries, could contribute to defragmenting the habitat for some species and mitigating the loss of biodiversity in highly humanized areas, such as intensive farming land. However, practitioners must implement a comprehensive management approach from design and construction phases to the later phases of management, taking into account objectives of improving the support of ecosystem services. Moreover, administrative bodies should manage the road network as a whole and with a long-term vision, moving away from short-sighted approaches focused only on specific projects.

ELECTRONIC APPENDICES

Electronic Appendix S1. Techniques used to determine each soil parameter.

Electronic Appendix S2. List of species found in the study. We are indicated the frecuency for each species in each scenario. For the species present in more than 20% of the plots in at least one scenario their preferences for any of the five scenarios considered is indicated.

Electronic Appendix S3. Fit of the descriptive variables of the community and soil variable to RDA model of species composition matrix constrained by environmental scenario.

Electronic Appendix S4. Fit of the descriptive variables of the community and soil variable to partial RDA model of species composition matrix constrained by environmental scenario, after removing variation caused by soil variables.

REFERENCES

Aedo, C., Medina, L., & Fernández-Albert, M. 2013. Species richness and endemicity in the Spanish vascular flora. *Nordic Journal of botany* 31: 478–488.

Andrés, P., & Jorba, M. 2000. Mitigation strategies in some motorway embankments (Catalonia, Spain). *Restoration Ecology* 8: 268–275.

Arenas, J.M., Escudero, A., Magro, S., Balaguer, L., & Casado, M.A. 2015. Woody colonization of road embankments: A large spatial scale survey in central Spain. *Landscape and Urban Planning* 141: 52–58.

Auffret, A.G., & Cousins, S.A.O. 2013. Grassland connectivity by motor vehicles and grazing livestock. *Ecography* 001–008.

Benton, T.G., Vickery, J. a., & Wilson, J.D. 2003. Farmland biodiversity: Is habitat heterogeneity the key? *Trends in Ecology and Evolution* 18: 182–188.

Breckwoldt, R. 1990. *Living corridors: conservation and management of roadside vegetation.* Greening Australia, Camberra.

Caballero, I., Olano, J.M., Loidi, J., & Escudero, A. 2008. A model for small-scale seed bank and standing vegetation connection along time. *Oikos* 117: 1788–1795.

CAM. 1992. Decreto 18/1992, Catálogo Regional de especies amenazadas de fauna y flora silvestres.

Castroviejo, S. 1986-2016. *Flora ibérica.* Real Jardín Botánico, CISC, Madrid.

Cerdà, A. 2007. Soil water erosion on road embankments in eastern Spain. *Science of the total environment* 378: 151–5.

De Cáceres, M., Legendre, P. 2009. Associations between species and groups of sites: indices and statistical inference. *Ecology* 90:3566–3574.

DOCM. 1998. *Decreto 33/1998, Catálogo regional de especies amenazadas de Castilla-La Mancha.*

Escudero, A., Palacio, S., Maestre, F.T., & Luzuriaga, A.L. 2014. Plant life on gypsum: a review of its multiple facets. *Biological rewiews* 90: 1–18.

European Commission. 2010. LIFE building up Europe's green infrastructure: Addressing connectivity and enhancing ecosystem functions.

Forman, R.T.T., & Alexander, L.E. 1998. Road and their major ecological effects. *Annual Review of Ecology and Systematics* 29: 207–231.

Gómez-Aparicio, L., Zamora, R., Gómez, J.M., Hódar, J.A., Castro, J., & Baraza, E. 2004. Applying plant facilitation to forest restoration: a meta-analysis of the use of shrubs as nurse plants. *Ecological Applications* 14: 1128–1138.

Gutiérrez, J.R., Arancio, G., & Jaksic, F.M. 2000. Variation in vegetation and seed bank in a Chilean semi-arid community affected by ENSO 1997. *Journal of Vegetation Science* 11: 641–648.

Helden, A.J., & Leather, S.R. 2004. Biodiversity on urban roundabouts-Hemiptera, management and the species-area relationship. *Basic and Applied Ecology* 5: 367–377.

Jiménez, M.D., Ruíz Capillas, P., Mola, I., Pérez-Corona, E., Casado, M.A., & Balaguer, L. 2013. Soil development at the roadside: a case study of a novel ecosystem. *Land Degradation & Development & Development* 24: 564–574.

Jones, C., Lawton, J., & Shachak, M. 1994. Organisms as ecosystem engineers. *Ecosystem Management* 69: 373–386.

Karp, D.S., Rominger, A.J., Zook, J., Ranganathan, J., Ehrlich, P.R., & Daily, G.C. 2012. Intensive agriculture erodes β-diversity at large scales. *Ecology Letters* 15: 963–970.

Kershaw, M., Williams, P., & Mace, G. 1994. Conservation of Afrotropical antelopes: consequences and efficiency of using different site selection methods and diversity criteria. *Biodiversity & Conservation* 3: 354–372.

Legendre, P., & Gallagher, E.D. 2001. Ecologically meaningful transformations for ordination of species data. *Oecologia* 129: 271–280.

Lugo, A.E., & Gucinski, H. 2000. Function, effects, and management of forest roads. *Forest Ecology and Management* 133: 249–262.

Luzuriaga, A.L., Sánchez, A.M., Maestre, F.T., & Escudero, A. 2012. Assemblage of a semi-arid annual plant community: abiotic and biotic filters act hierarchically. *PloS one* 7: e41270.

Maestre, F.T., Quero, J.L., Gotelli, N.J., Escudero, A., Ochoa, V., Delgado-Baquerizo, M., García-Gómez, M., Bowker, M. A, Soliveres, S., (...) & Zaady, E. 2012. Plant species richness and ecosystem multifunctionality in global drylands. *Science* 335: 214–8.

Melman, P., & Verkaar, H. 1991. Layout and management of herbaceous vegetation in road verges. In van Bohemen, H.D., Buizer, D.A.G., & Little, A. (eds.), *Nature engineering and civil engineering works*, pp. 62–78. Pudoc, Wageningen.

de Mendiburu, F. 2014. agricolae: Statistical Procedures for Agricultural Research.

Millennium Ecosystem Assessment. 2005. *Ecosystems and Human Well-being: Synthesis.* Island Press, Washington (DC).

MMAMM. 2011. *Real Decreto 139/2011. Listado de Especies Silvestres en Régimen de Protección Especial y del Catálogo Español de Especies Amenazadas.* Spain.

Mola, I., Jiménez, M.D., López-Jiménez, N., Casado, M. a., & Balaguer, L. 2011. Roadside Reclamation Outside the Revegetation Season: Management Options under Schedule Pressure. *Restoration Ecology* 19: 83–92.

Mota, J.F., Gomez, P.S., Merlo Calvente, M.E., Catalan Rodriguez, P., Lumbreras, E.L., de La Cruz Rot, M., Navarro Reyes, F.B., Gallardo, F.M., Esteban, C.B., (...) & Perez Garcia, F.J. 2009. Aproximación a la checklist de los gipsófitos ibéricos. *Anales de Biologia* 31: 71–80.

Münzbergová, Z., & Herben, T. 2005. Seed, dispersal, microsite, habitat and recruitment limitation: identification of terms and concepts in studies of limitations. *Oecologia* 145: 1–8.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., & Wagner, H. 2015. vegan: Community Ecology Package.

Parr, T., & Way, J. 1988. Management of roadside vegetation: The long-term effects of cutting. *Journal of Applied Ecology* 25: 1073–1087.

Perelman, S.B., Burkart, S.E., & León, R.J.C. 2003. The role of a native tussock grass (Paspalum quadrifarium Lam.) in structuring plant communities in the Flooding Pampa grasslands, Argentina. *Methods* 12: 225–238.

Polis, G. a, Hurd, S.D., Jackson, C.T., & Piñero, F.S. 1997. El Nino Effects on the Dynamics and Control of An Island Ecosystem in the Gulf of California. *Ecology* 78: 1884–1897.

R Core Team. 2015. R: A Language and Environment for Statistical Computing.

Reynolds, J.F., Smith, D.M.S., Lambin, E.F., Turner, B.L., Mortimore, M., Batterbury, S.P.J., Downing, T.E., Dowlatabadi, H., Fernández, R.J., (...) & Walker, B. 2007. Global desertification: building a science for dryland development. *Science* 316: 847–51.

Rivas-Martínez, S., Díaz, T.E., Fernandez-Gonzalez, F., Izco, J., Loidi, J., Lousã, M., & Penas, A. 2002. Vascular plant communities of Spain and Portugal: addenda to the syntaxonomical checklis of 2001. Part 1. *Itinera Geobotanica* 15: 5–992.

Spooner, P., & Smallbone, L. 2009. Effects of road age on the structure of roadside vegetation in south-eastern Australia. *Agriculture, Ecosystems & Environment* 129: 57–64.

Strijker, D. 2005. Marginal lands in Europe - Causes of decline. *Basic and Applied Ecology* 6: 99–106.

Tikka, P., Koski, P., Kivelä, R., & Kuitunen, M. 2000. Can grassland plant communities be preserved on road and railway verges? *Applied Vegetation Science* 3: 25–32.

Tormo, J., Bochet, E., & García-Fayos, P. 2009. Restauración y revegetación de taludes de carreteras en ambientes mediterráneos semiáridos: procesos edáficos determinantes para el éxito. *Ecosistemas* 18: 79–90.

Trombulak, S.C., & Frissell, C.A. 2000. Review of ecological effects of roads on terrestrial and aquatic communities. *Conservation Biology* 14: 18–30.

Wilby, A., & Shachak, M. 2004. Shrubs, granivores and annual plant community stability in an arid ecosystem. *Oikos* 106: 209–216.

Verheye, W.H., & Boyadgiev, T.G. 1997. Evaluating the land use potencial of gypsiferous soils from field edogenic characteristics. *Soil Use and Management* 13 : 97–103.

Zeng, S.-L., Zhang, T.-T., Gao, Y., Ouyang, Z.-T., Chen, J.-K., Li, B., & Zhao, B. 2011. Effects of road age and distance on plant biodiversity: a case study in the Yellow River Delta of China. *Plant Ecology* 212: 1213–1229.
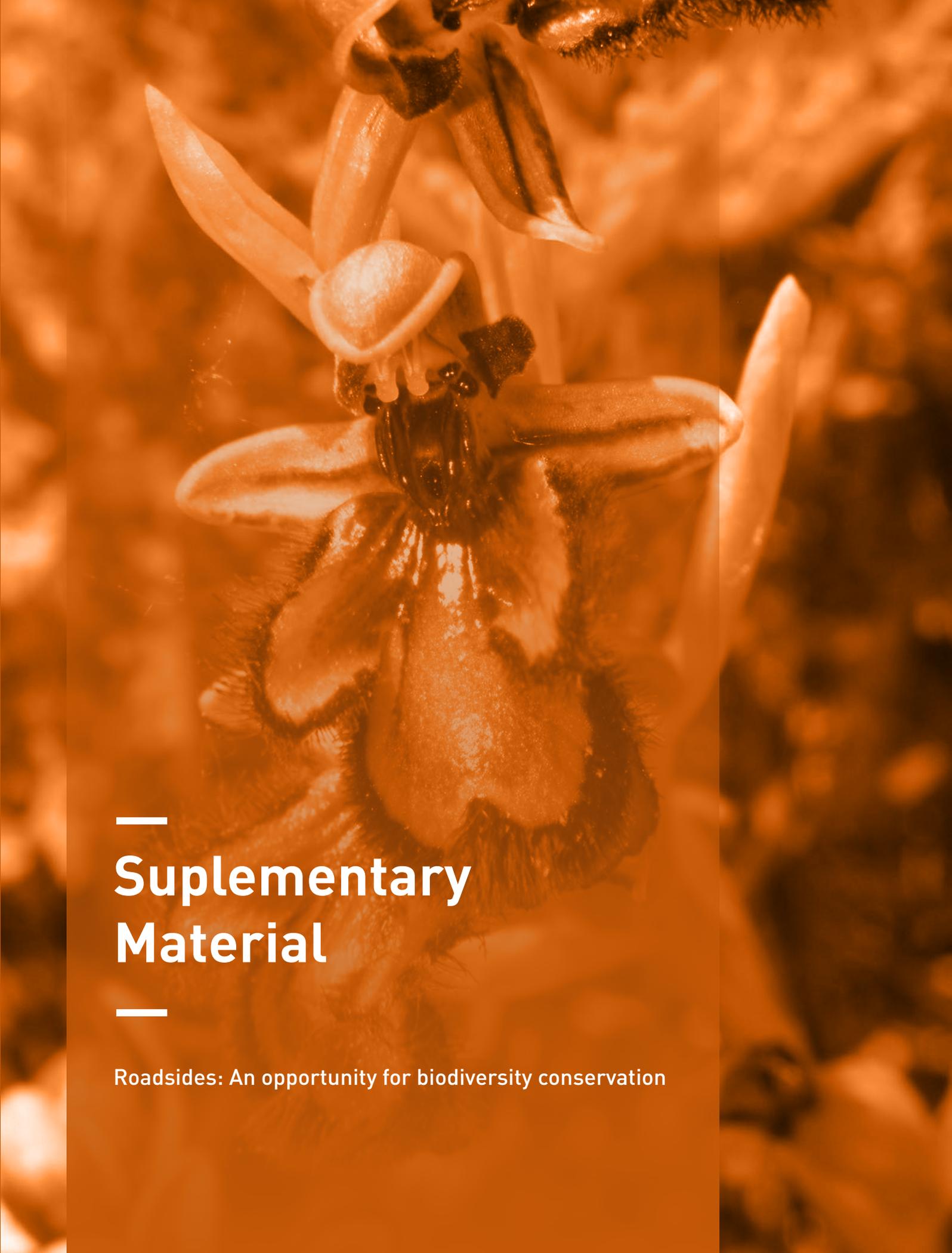
Suplementary Material

Roadsides: An opportunity for biodiversity conservation

Supporting information to the paper: Arenas, J.M. et al. "Roadsides: An opportunity for biodiversity conservation". Applied Vegetation Science.

Electronic Appendix S1. Techniques used to determine each soil parameter.

Organic C was determined by colourimetric techniques after oxidation with a mixture of potassium dichromate and sulphuric acid (Yeomans & Bremner 1988), total P and available N on a 19 SKALAR SAN++ Analyzer (Skalar, Breda, The Netherlands) after digestion with sulphuric acid and Kjedahl´s catalyst (Anderson & Ingram 1989). Potassium (K) was measured with the same analyser after the soil samples had been shaken with distilled water (1:5 ratio) for 1 h. Phosphatase and β-glucosidase activities were estimated by determination of the amount of p-nitrophenol released from 0.5 g soil after incubation at 37 C for 1 h, with the substrate p-nitrophenyl phosphate in MUB buffer (pH 6.5) for phosphatase activity (Tabatabai & Bremner 1969), and with the substrate 4-nitrophenyl-β-D- glucopyranoside in MUB buffer (pH 6.5) for glucosidase activity (Eivazi & Tabatabai 1988). All of these analyses were performed in the NUTRILAB laboratory of Rey Juan Carlos University (Madrid, Spain).

References

Anderson, J., & Ingram, J. 1989. *Tropical soil biology and fertility: A handbook of methods.* CAB International, Wallingford, Oxon, UK.

Eivazi, F., & Tabatabai, M. 1988. Glucosidases and galactosidases in soils. *Soil Biology and Biochemistry* 20: 601–606.

Tabatabai, M., & Bremner, J. 1969. Use of p-nitrophenyl phosphate for assay of soil phosphatase activity. *Soil biology and biochemistry* 1: 301–307.

Yeomans, J.C., & Bremner, J.M. 1988. A rapid and precise method for routine determination of organic carbon in soil. *Communications in Soil Science and Plant Analysis* 19: 1467–1476.

Supporting information to the paper: Arenas, J.M. et al. "Roadsides: An opportunity for biodiversity conservation". Applied Vegetation Science.

Electronic Appendix S2. List of species found in the study. For the species present in more than 20% of the plots in at least one scenario their preferences for any of the five scenarios considered were tested (Indicspecies package: Correlation index). For each species the frequency in each scenario are shown: FL-M: Natural matrix in fragmented landscape, FL-Em: Embankments in fragmented landscape, FL-Rc: Roadcut in fragmented landscape, UFL-M: Natural matrix in unfragmented landscape, UFL-Rv: Flat roadverges in unfragmented landscape. The scenarios significantly associated to each species ($p < 0.05$) are highlighted in bold. Each species is also characterized as nutrient demanding, gypsum tolerance (1: waifs; 2: gypsovags; 3: gypsophiles), Iberian endemicity or included in the National or Regional Catalogue of Endangered Species. * indicates the species that are present only in plots of natural vegetation (FL-M or UFL-M). ** indicates the species that are present only in roadsides (FL-Em, FL-Rc or UFL-Rv).

Species	p	FL-M	FL-Em	FL-Rc	UFL-M	UFL-Rv	Nutrient demanding	Gypsum tolerance	Endemic	Protected
Species present in more than 20% of the plots in at least one scenario										
Allium paniculatum	0.061	0.46	0.00	0.00	0.25	0.20	no	1	no	no
Allium sphaerocephalon	0.008	**0.62**	0.00	0.22	0.15	0.00	no	1	no	no
Antirrhinum graniticum	0.001	0.00	0.00	0.00	0.10	**0.80**	no	2	no	no
Artemisia campestris **	0.002	0.00	**0.50**	**0.44**	0.00	0.00	no	1	no	no
Artemisia herba-alba **	0.069	0.00	0.25	0.33	0.00	0.20	yes	1	no	no
Asphodelus ramosus	0.002	**0.64**	0.00	0.11	**0.65**	0.20	no	1	no	no
Astragalus incanus	0.003	**0.58**	0.00	0.11	0.10	0.00	no	2	no	no
Avenula bromoides	0.079	0.10	0.38	0.44	0.00	0.20	no	2	no	no
Bituminaria bituminosa **	0.012	0.00	**0.25**	0.00	0.00	0.00	no	1	no	no
Carlina corymbosa **	0.021	0.00	**0.38**	0.11	0.00	**0.40**	yes	1	no	no
Centaurea aspera	0.004	0.04	**0.88**	**0.44**	0.00	0.20	yes	1	no	no
Centaurea hyssopifolia	0.001	0.34	0.25	0.56	**0.95**	**1.00**	no	3	yes	no
Centaurea ornata	0.216	0.42	0.38	0.22	0.00	0.40	yes	1	no	no
Chondrilla juncea	0.062	0.02	0.25	0.00	0.00	0.20	yes	1	no	no

Species										
Crocus sp.	0.002	**0.54**	0.00	0.00	**0.55**	0.20	no	1	no	no
Cynodon dactylon	0.044	0.06	**0.50**	0.11	0.05	0.20	no	1	no	no
Dactylis glomerata	0.006	0.08	**0.75**	**0.56**	0.05	**0.40**	no	1	no	no
Daucus carota **	0.098	0.00	0.25	0.11	0.00	0.00	yes	1	no	no
Dipcadi serotinum *	0.019	**0.24**	0.00	0.00	**0.40**	0.00	no	1	no	yes
Dittrichia viscosa	0.017	0.00	**0.38**	0.11	0.20	**0.60**	yes	1	no	no
Elymus sp.	0.123	0.02	0.25	0.11	0.00	0.00	no	2	no	no
Eryngium campestre	0.570	0.54	0.75	0.56	0.60	0.80	yes	1	no	no
Euphorbia nicaeensis	0.042	0.10	**0.25**	**0.44**	0.05	0.00	no	2	no	no
Euphorbia serrata	0.305	0.80	0.50	0.56	0.25	0.60	yes	1	no	no
Foeniculum vulgare **	0.001	0.00	**0.62**	0.11	0.00	**0.60**	yes	1	no	no
Ginandridis type *	0.002	**0.40**	0.00	0.00	0.00	0.00	no	1	no	no
Gladiolus communis *	0.001	**0.40**	0.00	0.00	**0.60**	0.00	no	2	no	yes
Gypsophila bermejoi	0.149	0.02	0.12	0.22	0.00	0.00	no	2	yes	yes
Gypsophila struthium	0.031	0.10	**0.62**	**0.56**	**0.55**	**0.80**	no	3	yes	no
Helianthemum hirtum	0.040	**0.56**	0.00	0.11	**0.35**	0.20	no	2	no	yes
Helianthemum squamatum	0.558	0.62	0.37	0.56	0.80	0.60	no	3	no	no
Helichrysum stoechas	0.006	0.06	**0.62**	**0.89**	0.05	0.40	no	1	no	no
Herniaria fruticosa	0.056	0.08	0.00	0.44	0.10	0.20	no	3	yes	no
Hippocrepis commutata	0.030	**0.50**	**0.38**	0.00	0.05	0.20	no	2	yes	no
Koeleria castellana	0.131	0.40	0.25	0.56	0.70	0.80	no	3	yes	no
Lactuca sp.	0.001	0.00	0.00	0.00	0.15	**0.60**	yes	1	no	no
Launaea fragilis	0.001	**0.64**	0.00	**0.56**	**0.95**	**0.80**	no	3	no	no
Lepidium subulatum	0.001	**0.96**	0.25	**1.00**	**1.00**	**1.00**	no	3	no	no
Limonium dichotomum	0.097	0.02	0.38	0.22	0.00	0.20	no	2	yes	yes
Limonium toletanum	0.149	0.00	0.12	0.22	0.10	0.40	no	1	yes	yes
Lithodora fruticosa	0.901	0.12	0.12	0.22	0.25	0.20	no	2	no	no
Macrochloa tenacissima	0.006	0.56	0.50	0.22	**0.90**	**1.00**	no	2	no	no
Marrubium vulgare **	0.003	0.00	**0.38**	0.00	0.00	0.00	yes	1	no	no
Matthiola fruticulosa	0.005	**0.62**	0.38	**1.00**	0.05	0.40	no	2	no	no
Medicago sativa	0.015	0.06	**0.38**	**0.33**	0.00	0.00	yes	1	no	no
Melica ciliata	0.137	0.00	0.38	0.11	0.20	0.40	no	1	no	no
Muscari neglectum	0.003	**0.56**	0.00	0.11	**0.45**	0.00	no	1	no	no
Onobrychis matritensis	0.043	**0.32**	0.00	0.11	0.00	0.00	no	2	yes	no
Ononis pusilla	0.322	0.12	0.37	0.22	0.10	0.40	no	1	no	no

Ononis spinosa	0.028	0.02	**0.38**	0.00	0.00	**0.20**	yes	2	no	no
Phomis lychnitis	0.013	0.12	**0.38**	0.00	0.00	0.00	no	1	no	no
Piptatherum miliaceum **	0.105	0.00	0.12	0.22	0.00	0.00	yes	1	no	no
Plantago albicans	0.016	**0.92**	**0.75**	**1.00**	0.50	0.40	no	2	no	no
Plantago lanceolata **	0.013	0.00	**0.50**	**0.22**	0.00	0.00	no	1	no	no
Plantago sempervirens **	0.005	0.00	**0.38**	0.00	0.00	0.00	no	1	no	no
Poa bulbosa	0.006	**0.98**	0.12	**0.67**	0.45	0.20	yes	1	no	no
Prunus dulcis	0.068	0.04	0.25	0.22	0.00	0.00	no	1	no	no
Ranunculus bulbosus	0.081	0.26	0.00	0.00	0.10	0.00	no	2	no	no
Rumex pulcher **	0.005	0.00	**0.25**	0.00	0.00	0.00	yes	1	no	no
Salvia verbenaca **	0.077	0.00	0.38	0.11	0.00	0.20	yes	1	no	no
Sanguisorba verrucosa	0.167	0.26	0.75	0.67	0.40	0.60	yes	1	no	no
Santolina chamaecyparissus **	0.011	0.00	**0.25**	0.00	0.00	0.00	yes	1	no	no
Scorzonera angustifolia	0.005	**0.40**	0.00	**0.33**	0.00	0.00	no	2	no	no
Scorzonera hispanica	0.005	**0.48**	0.00	0.00	0.00	0.20	no	1	no	no
Sedum gipsicola	0.001	0.12	0.00	0.22	**0.70**	**0.80**	no	3	no	no
Stipa barbata	0.089	0.26	0.38	0.22	0.00	0.00	no	1	no	no
Stipa lagascae	0.306	0.68	0.37	0.78	0.80	0.60	no	1	no	no
Stipa parviflora	0.244	0.02	0.25	0.44	0.10	0.20	no	2	no	no
Taraxacum gr ovovatum	0.214	0.28	0.12	0.00	0.00	0.20	yes	1	no	no
Taraxacum gr. officinale	0.361	0.06	0.25	0.11	0.05	0.00	yes	1	no	no
Teucrium capitatum	0.446	0.34	0.12	0.22	0.50	0.40	no	2	no	no
Teucrium pumilum	0.142	0.02	0.00	0.11	0.25	0.00	no	3	yes	no
Thapsia villosa	0.020	**0.98**	0.75	0.56	**1.00**	**1.00**	no	1	no	no
Thymus lacaitae	0.267	0.24	0.38	0.44	0.75	0.40	no	3	yes	no
Thymus vulgaris	0.023	0.02	**0.38**	**0.22**	0.00	0.00	no	2	no	no
Thymus zygis	0.008	**0.74**	**0.75**	0.22	**0.95**	**0.80**	no	2	no	no
Verbascum sinuatum	0.019	0.00	**0.38**	0.00	0.05	**0.40**	yes	1	no	no

Species present in less than 20% of the plots in at least one scenario

Andryala ragusina	-	0.02	0.00	0.00	0.00	0.20	no	1	no	no
*Anemone palmata**	-	0.02	0.00	0.00	0.00	0.00	no	1	no	no
Arenaria cavanillesiana	-	0.08	0.00	0.11	0.00	0.00	no	3	yes	yes
*Aristolochia pistolochia**	-	0.02	0.00	0.00	0.00	0.00	no	1	no	no
Atractylis humilis	-	0.14	0.13	0.11	0.00	0.00	yes	2	no	yes

Bupleurum fruticescens	-	0.02	0.13	0.00	0.00	0.00	no	2	yes	no
Compositae 1*	-	0.04	0.00	0.00	0.00	0.00	-	-	-	-
Compositae 2*	-	0.04	0.00	0.00	0.00	0.00	-	-	-	-
Convolvulus arvensis**	-	0.00	0.13	0.11	0.00	0.20	yes	1	no	no
Convolvulus lineatus	-	0.08	0.00	0.11	0.00	0.00	yes	2	no	no
Coris monspeliensis	-	0.00	0.00	0.11	0.10	0.00	no	1	no	no
Doricnium pentaphyllum**	-	0.00	0.13	0.00	0.00	0.00	no	2	no	no
Echinops ritro**	-	0.00	0.13	0.00	0.00	0.00	yes	2	no	no
Ephedra nebrodensis*	-	0.02	0.00	0.00	0.05	0.00	no	2	no	no
Euphorbia characias**	-	0.00	0.00	0.11	0.00	0.00	no	1	no	no
Ferula communis**	-	0.00	0.13	0.11	0.00	0.00	yes	2	no	no
Frankenia thymifolia	-	0.02	0.00	0.11	0.10	0.00	no	2	no	no
Gagea lacaitae*	-	0.06	0.00	0.00	0.00	0.00	no	2	no	no
Genista scorpius*	-	0.02	0.00	0.00	0.00	0.00	no	2	no	no
Helianthemum cinereum	-	0.02	0.13	0.00	0.05	0.00	no	2	no	no
Helianthemum marifolium*	-	0.02	0.00	0.00	0.00	0.00	no	2	yes	yes
Hypericum perforatum**	-	0.00	0.13	0.00	0.00	0.00	yes	1	no	no
Lavandula latifolia*	-	0.02	0.00	0.00	0.00	0.00	no	1	no	no
Linum suffruticosum	-	0.02	0.13	0.00	0.00	0.00	no	2	no	no
Lygeum spartum**	-	0.00	0.00	0.11	0.00	0.00	no	1	no	no
Mercurialis tomentosa**	-	0.00	0.13	0.00	0.00	0.00	yes	1	no	no
Ononis natrix**	-	0.00	0.13	0.00	0.00	0.00	yes	1	no	yes
Ononis tridentata	-	0.04	0.00	0.11	0.05	0.00	no	3	no	no
Ononis viscosa**	-	0.00	0.13	0.00	0.00	0.00	yes	2	no	no
Ophrys speculum	-	0.02	0.13	0.00	0.00	0.00	no	1	no	no
Ornitogalum narbonense*	-	0.06	0.00	0.00	0.00	0.00	no	1	no	no
Orobanche elatior	-	0.06	0.00	0.11	0.00	0.00	no	1	no	no
Orobanche ramosa*	-	0.12	0.00	0.00	0.00	0.00	no	1	no	yes
Phragmites australis**	-	0.00	0.13	0.00	0.00	0.00	no	1	no	no
Pinus halepensis**	-	0.00	0.13	0.11	0.00	0.00	no	1	no	no
Podospermun lacineata**	-	0.00	0.13	0.11	0.00	0.00	no	1	no	no
Quercus coccifera*	-	0.00	0.00	0.00	0.15	0.00	no	1	no	no
Quercus rotundifolia	-	0.00	0.00	0.00	0.10	0.20	no	1	no	no
Retama sphaerocarpa	-	0.02	0.00	0.00	0.10	0.20	no	2	no	no
Rhaponticum coniferum**	-	0.00	0.13	0.11	0.00	0.20	no	1	no	no

*Rubia peregrina***	-	0.00	0.00	0.00	0.00	0.20	no	1	no	no
*Salsola vermiculata***	-	0.00	0.00	0.11	0.00	0.20	yes	1	no	no
*Salvia aegyptiaca***	-	0.00	0.00	0.00	0.00	0.20	no	1	no	no
*Salvia lavandulifolia**	-	0.00	0.00	0.00	0.10	0.00	no	2	no	no
*Schoenus nigricans***	-	0.00	0.00	0.11	0.00	0.00	no	1	no	no
Sedum album	-	0.00	0.13	0.00	0.05	0.00	no	1	no	no
*Senecio gr. jacobaea***	-	0.00	0.13	0.00	0.00	0.00	yes	1	no	no
Sideritis hirsuta	-	0.06	0.13	0.00	0.00	0.00	yes	1	no	no
Sonchus crassifolius	-	0.00	0.00	0.00	0.10	0.20	no	1	no	no
Stipa atlantica	-	0.02	0.00	0.11	0.00	0.20	no	1	no	no
*Tamarix parviflora***	-	0.00	0.00	0.11	0.00	0.00	no	1	no	no
Teucrium pseudochamaepitis	-	0.02	0.00	0.11	0.00	0.00	yes	2	no	no
*Ulmus pumila***	-	0.00	0.13	0.11	0.00	0.00	no	1	no	no

Supporting information to the paper: Arenas, J.M. et al. "Roadsides: An opportunity for biodiversity conservation". Applied Vegetation Science.

Electronic Appendix S3. Fit of the descriptive variables of the community and soil variable to RDA model of species composition matrix constrained by environmental scenario.

	RDA1	RDA2	R2	P
Descriptive variables of the community				
Perennial total cover	-0.961	-0.276	0.045	0.130
Species richness	-0.073	-0.997	0.043	0.129
Inverse Simpson's index	0.924	-0.381	0.119	0.001
Number of protected species	-0.748	0.664	0.109	0.005
Number of endemic species	0.955	0.295	0.247	0.001
Number of nutrient demanding species	0.272	-0.962	0.476	0.001
Gypsophily index	0.694	0.720	0.616	0.001
Restricted-range diversity	0.493	-0.870	0.411	0.001
Soil variables				
β-Glucosidase	-0.683	-0.730	0.360	0.001
Acid phosphatase	-0.243	-0.970	0.255	0.001
Nitrogen	-0.922	0.387	0.198	0.002
Phosphorus	-0.424	-0.906	0.136	0.001
Potassium	0.161	-0.987	0.255	0.001
Electric conductivity	0.328	0.945	0.501	0.001
Organic carbon	-0.822	0.570	0.161	0.002
pH	-0.120	-0.993	0.267	0.001

Supporting information to the paper: Arenas, J.M. et al. "Roadsides: An opportunity for biodiversity conservation". Applied Vegetation Science.

Electronic Appendix S4. Fit of the descriptive variables of the community and soil variable to partial RDA model of species composition matrix constrained by environmental scenario, after removing variation caused by soil variables. According soil variables selection explained in the manuscript, we only removed the variation caused by six soil variables (B-Glucosidase, Acid phosphatase, Nitrogen, Phosphorus, Potassium and Electric conductivity).

	RDA1	RDA2	R2	P
Descriptive variables of the community				
Perennial total cover	0.999	0.003	0.004	0.854
Species richness	-0.537	-0.844	0.021	0.393
Inverse Simpson's index	0.509	-0.861	0.064	0.057
Number of protected species	-0.833	0.553	0.036	0.164
Number of endemic species	0.948	-0.320	0.079	**0.029**
Number of nutrient demanding species	0.619	-0.786	0.062	0.060
Gypsophily index	0.959	-0.284	0.058	0.077
Restricted-range diversity	0.647	-0.763	0.122	**0.007**
Soil variables				
β-Glucosidase	-	-	0.000	1.000
Acid phosphatase	-	-	0.000	1.000
Nitrogen	-	-	0.000	1.000
Phosphorus	-	-	0.000	1.000
Potassium	-	-	0.000	1.000
Electric conductivity	-	-	0.000	1.000
Organic carbon	0.995	-0.098	0.006	0.773
pH	0.657	-0.754	0.023	0.344

—

Capítulo 5

Motorway influence, landscape fragmentation and soil properties: landscape and fine scale determinants of perennial plant diversity in a gypsum ecosystem

—

J.M. Arenas, A. Escudero, I. Mola, M.A. Casado.

(En preparación)

Motorway influence, landscape fragmentation and soil properties: landscape and fine scale determinants of perennial plant diversity in a gypsum ecosystem.

Juan M. Arenas [a] [*], Adrián Escudero[b], Ignacio Mola[c], Miguel A. Casado[a].

[a] Departamento de Ecología, Universidad Complutense de Madrid, 28040 Madrid, Spain

[b] Unidad de Biodiversidad y Conservación, Departamento de Biología y Geología, Universidad Rey Juan Carlos, Móstoles, 28933 Madrid, Spain

[c] Research, Development and Innovation (R&D) Service, Obrascón Huarte Lain, S.A. (OHL), 28046 Madrid, Spain

[*] Author for correspondence:
   jmarenas@ucm.es

· ··

ABSTRACT

In this study, we analyzes jointly the effects the site characteristics, the habitat fragments variability and the possible negative or positive effects produced by a motorway on the natural vegetation in a fragmented territory with a high ecological value. We selected 50 remnants of gypsum vegetation embedded in an agricultural matrix. In each remnant we sampled perennial vegetation, as well as potential predictors of community behavior both at soil scale and at landscape scale, including the distance to a motorway. To describe plant communities, we focus on 13 variables grouped in: functional group (i.e. degree of soil specialization and dispersion syndromes), taxonomic diversity (i.e. within-fragment diversity and among fragment diversity) and community structure (i.e. species co-occurrences and floristic composition). We used Multi-Model Inference analyses to determine the drivers that best explained each of the response variables analyzed. The best-modeled response variables are the floristic composition (69%) and gypsum tolerance (66%) of the community, followed by local contribution to beta diversity (37%) of each remnant and cover of nutrient-demanding species (36%). These gypsophilous communities studied are mainly organized according to variables that act both locally (edaphic) and landscape scale. However, predictors at landscape scale ultimately affect soil quality. Moreover, we have not found positive or negative effects of motorway on the community. To conclusion, we recommended to practitioners that the ecological restoration of degraded fragments should focus on recovering soil characteristics to recover typical gypsum communities, without neglecting improvements in connectivity that increase functionality and resilience at the landscape scale.

INTRODUCTION

Fragmentation is one of the most relevant and pervasive drivers of global biodiversity change (Wilson 1989; Saunders et al. 1991; Young et al. 1996). Its occurrence is especially noticeable in high income countries where agricultural practices have historically transformed the landscape into patches or remnants (*sensu* Saunders et al. 1991) of natural vegetation of different sizes interspersed among crops. The consequences of this fragmentation on plant communities, and in particular on their taxonomic diversity, have mainly been related to the size and degree of isolation (or connectivity) of patches (Turner 1996; Harrison 1999; Bruun 2000; Debinski & Holt 2000). Habitat availability for many organisms decreases with area, and consequently, abundance will be smaller and populations will be submitted to the pernicious effect of small population sizes and the corresponding increase of local extinction risk. In addition, isolation and loss of connectivity between communities can increases the effects of the habitat loss itself (Fahrig 2013).

The construction of motorways and other linear infrastructures is, along with agricultural practices, one of the major disruptor of habitat connectivity (Forman & Alexander 1998; Fu et al. 2010). In fact, Forman (2000) estimated that 19% of the total area of the United Stated of America is ecologically affected by the road network. This road barrier can adversely affect not only animal movements, but also different biotic and abiotic ecological flows (Forman & Alexander 1998; Trombulak & Frissell 2000; Coffin 2007). However, its negative effect could be counteracted for particular species and some ecological flows due to the fact road verges could improve habitat and ecological connectivity (*sensu* Lindenmayer & Fischer 2007). These unexpected positive effects are based mainly on two arguments. On one hand, the road verges can offer new opportunities for the establishment of many plant species in this novel and emergent ecosystems (Bochet et al. 2007; de la Riva et al. 2011; Arenas et al. 2017). In this line, we have found

such an ecosystem service (see chapter 4 in this thesis) which concurs with diverse studies highlighting the role of road verges as species refuges (Tikka et al. 2000; Spooner & Smallbone 2009). On the other hand, there are studies that show that the road margins serve as a corridor for some species so increasing the connectivity at the landscape scale (Tikka et al. 2001). Thus, in the context of a fragmented landscape, the motorway network can have a double effect, reducing connectivity among landscape patches for some species, and increasing it for others. With this in mind, a traditional agricultural landscape crossed by a motorway can result in contrasting, additive, synergic and even negative effects on community composition and species diversity and may alter assembly mechanisms at different spatial scales.

The effects of landscape fragmentation (e.g. connectivity, patch area or patch history which is related to the changes of size and connectivity along time) and road network on plant diversity and community assembly interact with other factors that determine the plant community at local-scale (e.g. soil nutrients, microclimate). This influence of local factors on the features of plant communities is especially noticeable in habitats associated to edaphically stressful soils for plant growth, such as serpentine (Brooks 1987; Anacker 2014) or gypsum soils (Escudero et al. 2014). In this sense, perennial plant species housed in remnants of semi-arid Mediterranean agrosystems in gypsum soil islands are an ideal model for assessing the effects of local and regional factors on plant community assembly. Firstly, gypsophile vegetation is strongly restricted by the physical and chemical limitations imposed by gypsum soils (Escudero et al. 2014), therefore it is a type of vegetation appropriate to study the effects at fine scale. Secondly, perennial vegetation is persistent over time, with low dependence on weather conditions of each year and allows more structured and stable communities. Thirdly, primary plant succession in gypsum habitats is a slow process (Escudero et al. 2014),

so in these zones there are no complex dynamics of fast growing species in abandoned areas, which would complicate the interpretation of assembly mechanisms (Del Castillo 2015). Finally, gypsum habitats are an European conservation priority (see European Directive for Conservation of Habitats and Wild Fauna and Flora; Directive 92/43/CEE, 1992), therefore the studies in these habitats can help to develop conservation and restoration policies.

Here, we jointly evaluated the effects of both local scale (i.e., soil characteristics) and landscape-scale factors (i.e., remnant habitat characteristics and the possible effects produced by a motorway) on perennial plant communities in a fragmented gypsum territory. Most of the studies that analyze the fragmentation in plant communities have focused mainly on its effect on the species richness and, to a lesser extent, on the floristic composition (Quintana-Ascencio & Menges 1996) or some species traits, such as the type of dispersion (Grashof-Bokdam 1997; Honnay et al. 2002; Maurer et al. 2003; Piessens et al. 2005). However, these local and landscape scale factors can have consequences not only on species richness but also on other structural or functional aspects of the community. To describe their effects on plant communities, we focus on three sets of variables related to: a) functional group, b) taxonomic diversity and c) community structure. The functional groups are established considering both the degree of soil specialization of the community and the dispersion syndromes. Soil specialists are related to the ability to establish and grow of the species, and depend on soil characteristics at the site scale, whereas dispersion are related to the ability to arrive and depends more on landscape characteristics, such as connectivity and distances. Taxonomic diversity can be focused on two spatial scales: at local scale (alpha diversity and within remnant beta diversity) and at landscape scale (contributions of each remnant to landscape beta diversity). Alpha diversity and within remnant beta diversity are associated to species

coexistence mechanisms at the site scale (Ricklefs 1987; López-Martínez et al. 2013), whereas beta diversity among remnants reports on the effect of fragmentation on metacommunity processes (Ricklefs 1987; Myers et al. 2013). Finally, the community structure refers to patterns of species coexistence and can be evaluated both at the species level (patterns of species co-occurrence by pairs; Gotelli 2000) and at the whole community level (e.g., axes of a multivariate ordination analysis). In both cases the patterns found are determined by the action of biotic factors such as interspecific competition, tolerance, or facilitation (Diamond 1975; Geho et al. 2007) as well as abiotic filter (e.g., environmental conditions; Keddy 1992).

Our working hypothesis is that the characteristics of the plant communities (i.e., functional groups, taxonomic diversity, and community structure) in fragmented landscapes are the result of joint action of fine scale soil factors and landscape-scale variables, including the distance between remnants and motorway. Our expectations are that the existence of roads can have significant effects on plant communities on a regional scale, given their peculiar characteristics (new environmental conditions, increasing landscape heterogeneity, creation of novel habitats, etc.) and their role as reservoir and corridor for species (Tikka et al. 2000; Tikka et al. 2001; Spooner & Smallbone 2009). The possible expected effects of the motorway on the response variables analyzed in this study are shown in Table 1. Specifically, we try to answer the following questions: 1) Are the three groups of descriptors considered in this study (i.e., soil characteristics, landscape variables and effect of the motorway) driver in configuring communities? Due to gypsum vegetation is highly dependent on soil characteristics, we believe that this will be the key factor to configuring the community. 2) Which of the characteristics of the community (i.e., functional groups, taxonomic diversity or floristic composition) better synthesizes the response of the plant community as a whole? 3) Does the distance to the

Table 1. Possible positive expected effects of the motorways on the response variables analyzed in this study. ND: community weighted mean for nutrient-demanding species; GT: community weighted mean for the average gypsum tolerance; WD: community weighted mean for wind-dispersed species; AD: community weighted mean for animal-dispersed species; LS: community weighted mean for species with seeds lack structures; RRD: Restricted-range diversity; LCBD: Local Contribution to Beta Diversity; SES: Standardized Effect Size of C-score index of co-occurrence ; DCA: axes of a Detrended Correspondece Analysis.

ND	Embankments, and other road verges, are disturbed areas that favour the establishment of ruderal species. These species can reach fragments closest to the road, increasing the number of Nutrient demanding species.	Chapter 4 of this thesis. Frenkel (1970) Johnston & Johnston (2004)
GT	Roadcuts, due to its constructive characteristics, shelter species of low evolved and nutrient poor soils, such as gypsum soils. These species can reach the fragments closest to the road, causing an increase of gypsum tolerant species.	Chapter 4 of this thesis.
WD	On one hand, there are seed movements parallel to motorway due to dispersal of wind-dispersed seeds by the airflow of vehicles. On the other hand, motorways can modify the wind flows causing accumulation of wind-dispersed seeds in the surroundings of the roads	von der Lippe et al. (2013)
AD	Roadside verges in intensively grazed Mediterranean landscapes act as important refuges for small mammals and they can improve. Moreover, isolated trees in road verges can act as dispersal point for disperser. Both processes improve the animal movements parallel to the road facilitating the dispersion of animal-dispersed plants to other areas close to the road.	Sabino-Marques & Mira (2011) Coulson et al. (2013) Arenas et al, (2017)
LS	No hypothetical effect	
Species richness	The high environmental heterogeneity of road slopes can increase species richness. The nearest fragments may receive a greater number of species from these road slopes.	Jakobsson et al. (2016) Chapter 4 of this thesis.
Turnover species index	No hypothetical effect	
Nestedness Index	No hypothetical effect	
RRD	Road slopes accumulate more species of restricted distribution range. These species could reach the fragments closer to the road and increase their RRD.	Tikka et al. (2000) Chapter 4 of this thesis.
LCBD	See Richness and RRD.	Jakobsson et al. (2016) Tikka et al. (2000) Chapter 4 of this thesis.
SES	A constant flow of species and individuals from sources such as road verges to a fragment may modify the relationships between species found in this fragment.	
DCA	If the fragments closest to a motorway receive a constant flow of individuals, and even new species, the community structure will be modified.	

road have any effect on the composition and structure of the plant community of the remnants? By addressing these questions, we seek to increase the knowledge needed to improve the conservation and ecological restoration of gypsum communities in fragmented agricultural landscape, as well as to know the role of road verges in flows channeling into these fragmented landscapes and the implications that this would have for practitioners and researchers.

MATERIAL AND METHODS

Study area

The present study was developed in the surrounding area of the A3 motorway, in central Spain, on the border between Madrid and Castilla-La Mancha autonomous regions (40º 5′ 52′′ N, 3º 7′ 52′′ W and 40º 2′ 5′′ N, 3º 2′ 40′′ W). This road was formerly a national road (N3 Madrid-Valencia) for the last 60 years, and it has been operative

as a motorway at least the last 30 years. The study area comprises 3 km at both sides of the motorway along 13 km. This area is an agricultural fragmented landscape, with natural vegetation remnants immersed in a cropland matrix (Fig. 1). Soils are predominantly typical gypsiorthid with high gypsum soil content (over 80%). The dominant vegetation in remnants are gypsophilous communities represented by shrubs of the genera *Thymus* and *Helianthemum,* and by the tussock forming grass *Stipa tenacissima* and other perennial plants, such as *Poa bulbosa,* L*epidium subulatum* and *Plantago albicans.* This perennial vegetation is interspersed, in open areas, with a well-developed biological soil crust and highly diverse ephemeral plant communitys. The climate is semi-arid Mediterranean with a mean annual rainfall of 455 mm, and average annual temperatures of 14.15ºC (Ninyerola et al. 2005). Seasonal distribution of the precipitation shows major rainfall periods in early spring and late autumn and extremely intense summer drought.
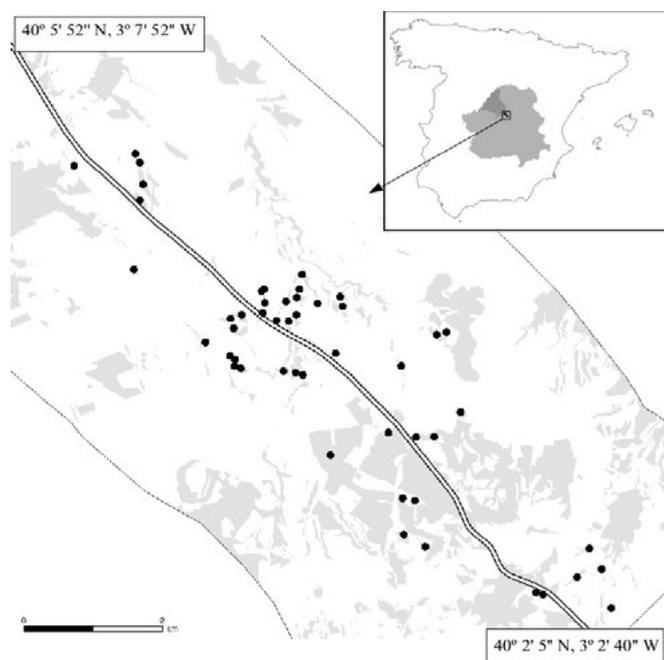

Figure 1. Study area. Location of the 50 sampling plots on the A-3 motorway Madrid-Valencia (central Spain). In the Spain map, dark grey and light grey areas represents Madrid and Castilla-La Mancha autonomous regions, respectively. In the site map, the light gray colour corresponds to remnants of natural vegetation.

Sampling design and explicative variables

We selected 50 remnants representative of a wide range of sizes and distances to the road. We established a 20 x 20 m sampling plot in each of them, rejecting communities dominated by tussock grass *Stipa tenacissima.* Each plot was geo-referenced, taking the coordinates in its centre. The distance from the plot to the motorway was measured using the open source software Quantum GIS (QGIS Development Team 2013).

Each remnant was characterized considering its area, history and connectivity. High-resolution aerial photographs taken by the Aerial Orthophotography National Plan of the National Geographic Institute of Spain (2011) were digitalized and used to calculate remnant area by the software Quantum GIS. Remnant area ranged from 0.05 to 101 ha. The area was log-transformed to linearize the effect of very large remnants. To characterize remnants history, we also used aerial photographs taken in 1984 and 2011 by the Aerial Orthophotography National Plan of the National Geographic Institute of Spain. Remnant history was divided in three categories: stability ("S") when changes of the remnant area between both years were less than 30% (18 plots), decrease ("D") when the area was reduced by more than 30% (26 plots) and increase ("I") when the area was increased by more than 30% (6 plots). Remnant connectivity was quantified using a proximity index that accounts for the number of surrounding remnants weighted by their distance to the target remnant (Matesanz et al. 2015):

$$C_i = \log_{10} \sum_{k=1}^{n} A_k / d_{ik}^2, i \neq k$$

where C_i is the connectivity of remnant i, n is the total number of surrounding remnants within a 500 m radius from the remnant i, A_k is the area of the remnant k, and d_{ik} is the minimum distance between remnants i and k. Neighbour remnants to estimate connectivity were placed in a larger area of 13 x 6 km. With this connectivity predictor we only wanted to consider the agriculture fragmentation driver, thus, all the remnants were considered without differences between the two

sides of the motorway and considering that the road is not a barrier.

In the centre of each plot slope and aspect were measured. Slope, aspect and latitude were used for calculate the "Soil Heat Load" using the equations described by McCune and Keon (2002). Seven soil variables were measured in each plot: ß-glucosidase, acid phosphatase, total organic carbon, total nitrogen, total phosphorus, potassium and pH. For it, six soil cores per plot (5 cm in diameter and 10 cm deep) were collected, three in bare zones and three under shrub canopy, excluding the aboveground biomass and litter. The cores were taken in August when the soil was dry, were air dried for one month and sieved through a 2 mm mesh. ß-glucosidase and acid phosphatase activities were estimated by determination of the amount of p-nitrophenol released from 0.5 g soil after incubation at 37 C for 1 h, with the substrate p-nitrophenyl phosphate in MUB buffer (pH 6.5) for phosphatase activity (Tabatabai & Bremner 1969), and with the substrate 4-nitrophenyl-ß-D- glucopyranoside in MUB buffer (pH 6.5) for glucosidase activity (Eivazi & Tabatabai 1988). Total organic carbon was determined by colorimetric techniques after oxidation with a mixture of potassium dichromate and sulfuric acid (Yeomans & Bremner 1988), and total phosphorus and available total nitrogen on a 19 SKALAR SAN++ Analyzer (Skalar, Breda, The Netherlands) after digestion with sulfuric acid and Kjedahl´s catalyst (Anderson & Ingram 1989). Potassium was measured with the same analyser after the soil samples had been shaken with distilled water (1:5 ratio) for 1 h. All of these analyses were performed in the NUTRILAB laboratory of Rey Juan Carlos University (Madrid, Spain). We calculated a weighted mean value per variable at the plot level considering the samples taken in bare zones and under shrub canopy, weighted by the mean value of perennial plant cover of the plot. Since both "slow variables" (sensu Reynolds et al. 2007) -total organic carbon, total nitrogen, total phosphorus, and potassium- and the two "rapid variables" (soil

enzyme activities: ß-glucosidase and acid phosphatase) are determinants of the functioning of ecosystems (Reiss et al. 2009; Jax 2010), we calculated a soil multifunctionality index (M) per plot (Maestre et al. 2012). We first calculated the Z scores (standardized deviates) of the 6 soil parameters at the plot scale. Then we averaged the Z scores of all variables to obtain the multifunctionality index as surrogate of soil productivity for each plot. The pH was not included in the multifunctionality index, and it was used as another independent variable.

Vegetation sampling and response variables

Inside each of the 50 plots, five 2.4 x 2.4 m quadrats were surveyed, four in the corners and the fifth in the centre of the plot. Total perennial plant cover was visually estimated for each quadrat and the average of the five quadrats per plot was calculated. The percentage cover of each perennial plant species was also visually estimated for each quadrat. Random survey walks inside the plot, taking note of those species that had not appeared in the five quadrats, complemented the sampling. Finally, the percentage cover of each plant was calculated as the average of the 5 quadrats, adding 0.1% to the species identified only in random walk surveys. Moreover, the central quadrat was divided in 64 cells (30 x 30 cm) to analyze the species co-occurrence at microsite scale. In each cell, we surveyed presence/absence of each species. These samples were conducted in the spring of 2013, during the phenological peak of flowering for the studied community.

Data of the vegetation survey was used to calculate different sets of variables related to functional groups, taxonomic diversity and community structure. To describe the perennial community according to functional groups each species were characterized considering two soil features (i.e., gypsum tolerance and nutrient-demanding level), as well as by its main dispersion syndrome (i.e. wind, animal or without dispersal specialized structures) based on the

characteristics of propagules. The gypsum tolerance of each species was classified into one of three classes: plants that are rare on gypsum soils (1: waifs), plants that grow both on and off gypsum soils (2: gypsovags) and plants growing exclusively on gypsum soils (3: gypsophiles) (Mota et al. 2009; Castroviejo 1986-2014). The community weighted mean for the average gypsum tolerance (GT) of the species of each plot was estimated using:

$$GT = \sum_{sp=1}^{n} GT_{sp} * Cover_{sp} / \sum_{sp=1}^{n} Cover_{sp}$$

where GT_{sp} is the gypsum tolerance of each species (1: waifs; 2: gypsovags; 3: gypsophiles), $Cover_{sp}$ is the estimated cover of each species and n is the species richness in each plot. GT can range between 1 (all species of a plot are waifs) and 3 (all species are gypsophiles). Nutrient-demanding classification (with two categories: nutrient-demanding and non-nutrient-demanding species; sensu Castroviejo 1986-2014 and Rivas-Martínez et al. 2002) represents the species' capacity to grow in soils with high nutrient availability (indicative of disturbance and human-driven alterations) or low nutrient availability, respectively. The community weighted mean for nutrient-demanding (ND) was estimated in the same way that GT, replacing GT_{sp} by ND_{sp}, where ND_{sp} has two levels (1: nutrient-demanding species; 0: non-nutrient-demanding species). For main dispersion syndrome, each species was classified in one of the following categories according to the characteristics of their dispersal unit (seeds or fruits): wind-dispersed species, animal-dispersed species or species lacking specialized dispersal structures. We calculated the community weighted mean for wind-dispersed species (WD), the community weighted mean for animal-dispersed species (AD) and the community weighted mean for species lacking structures associated with specific dispersal mechanisms (LS).

The taxonomic diversity of each plot was analyzed at three levels: species richness of the plot (alpha diversity), beta diversity between the quadrats within

the plot (plot level) and the contributions of each plot to the landscape/regional beta diversity. Species richness per plot was the cumulative number of species of the five subplot, adding the species found in random survey walks. In order to assess beta diversity within the plot, we computed the two Baselga´s beta diversity components (Baselga 2010). Baselga´s beta diversity can account for the partition of total beta diversity into two additive components: patterns of beta diversity caused by species turnover and by nestedness. Turnover is the replacement of some species by others from quadrat to quadrat within a plot. Nestedness occurs when species assemblages of species-poor quadrats are subsets of those species present in richer ones. Turnover and nestedness were calculated using the functions "ct" and "cn", respectively, from "MBI" package for R (Chen 2012; R Core Team 2015). Finally, the contribution of each plot to landscape beta diversity was estimated using two different parameters: Restricted-Range Diversity (RRD) and Local Contribution to Beta Diversity (LCBD). RRD indicates the floral uniqueness of a plot in relation to other plots. To derive this index for each plot, the inverse numbers of sites in which each species occurs are summed, expressing this sum as a percentage of the total scores for all the species in the data set (Kershaw et al. 1994). A high value of restricted-range diversity indicates greater number of rare species on one plot. LCBD represent the degree of uniqueness of each sampling plot in terms of community composition. High LCBD values indicate the plots that contribute more than the mean to beta diversity at landscape level. LCBD was calculated using the Hellinger dissimilarity coefficients for the "cover x species" matrix by means of the "beta.div" function of (Legendre & De Cáceres 2013).

Finally, as community structure variables we considered both species co-occurrence index and floristic composition. The survey of the prensence-ausence in the 64 cells of the central quadrat was used to calculated the average C-score (Checkerboard score; Stone & Roberts

1990) of each plot. Due to the fact that average C-score is highly dependent of species number of each plot, we calculated the "Standardized Effect Size" (SES) for each plot. The SES measures the statistical amount of deviation from random co-occurrence, as:

$$SES = I_{obs} - I_{sim} / SD_{sim}$$

where I_{obs} is the C-score observed, I_{sim} is the mean of 1000 C-score generated from the simulated null model and SD_{sim} is the standard deviation of this 1000 simulated communities. Assuming a normal distribution of deviations, 95% of the SES values should fall between -1.96 and +1.96. Large positive SES values (>1.96) indicate statistically significant species segregation. Large negative SES values (less than –1.96) indicate statistically significant species aggregation. To generate the simulated communities we selected the Fixed-Fixed algorithm (Gotelli 2000) in which the sum of the rows (species) and the sum of the columns (plots) in simulated matrices remain constant and equal to the original matrix. I_{obs}, I_{sim} and SD_{sim} were calculated using the "cooc_null_model" function in the "EcoSimR" R package (Gotelli et al. 2015; R Core Team 2015). In the case of floristic composition we calculated the first two axes of a Detrended Correspondence Analysis (DCA). DCA was performed using the "decorana" function in the "vegan" R package (Oksanen et al. 2015; R Core Team 2015).

Data analyses

We considered as response variables the five indices related to the functional groups, the five taxonomic diversity indices and the three indices of community structure. In each case we used simultaneously the three sets of predictors: effects of soil characteristics (i.e., soil heat load, pH and M), the habitat remnants variability (i.e., area, connectivity and history transformed as dummy variable with two states: I and D) and the possible effects produced by the motorway (distance to the road). In order to detect multicollinearity, the variance inflation factors (VIF; Brauner & Shacham 1998) for each predictor were

computed. In all cases VIFs reached values lower than 1.5, so all predictors were used in the models. We used Multi-Model Inference technique (MMI; Burnham & Anderson 2002) to determine the drivers that explained each of the response variables. For a detailed explanation of the MMI analysis, see Arenas et al. (2015) (Chapter 2 of this thesis). The MMI techniques only detect the relative importance of each predictor, so the direction of the effect (positive or negative) was determined by the model-averaged parameter estimate (Burnham & Anderson 2002). Moreover, we calculated the confidence intervals to the model-averaged parameter estimates (alpha risk = 0.1) to know which parameter estimates do not overlap with 0, and therefore, give it a clear positive or negative effect (see Supplementary material). The adjusted variance explained by the saturated model (model with all predictors) was used as a surrogate for the explained variance for each MMI model. MMI analyses were performed using "glmulti" R package (Calcagno 2013; R Core Team 2015).

RESULTS

In the present study, we registered 84 perennial species, two of them could only be identified at family level, so they were not considered. According to gypsum tolerance of each species, we found 37 waifs, 33 gypsovags and 12 gypsophils. The mean of GT considering all plots was 1.74 , ranging from 1.16 to 2.8. The variance explained by the saturated model for GT was the second highest in this study (R^2 = 0.66; Table 2). Remnant area, remnant connectivity and soil multifunctionality were very important descriptors to explain GT (W_x=0.946, 0.998 and 0.999, respectively). Both remnant area and connectivity had positive coefficients, whereas soil multifunctionality showed a negative estimator (Table 2 and Fig. 2). Moreover, the distance from the plot to the motorway and pH also had relatively high importance (W_x=0.62 and 0.8 respectively), but the range of variation of the estimators overlaps the 0 value (Table S2). Of

Table 2. Relative importance of the predictors (columns) for modelled response variables (rows) in the MMI models. The sign (+ or -) indicates whether the model-averaged parameter estimates is positive or negative. The predictors that the confidence intervals to the model-averaged parameter estimates do not overlap with 0 have been highlighted in bold (see Supplementary results). ND: community weighted mean for nutrient-demanding species; GT: community weighted mean for the average gypsum tolerance; WD: community weighted mean for wind-dispersed species; AD: community weighted mean for animal-dispersed species; LS: community weighted mean for species with seeds lack structures; RRD: Restricted-range diversity; LCBD: Local Contribution to Beta Diversity; SES: Standardized Effect Size of C-score index of co-occurrence. For each model the R^2 adjusted are shown in the last (grey) column.

| | | Distance to Road | Remnant characteristics | | | | Soil characteristics | | | R^2 |
			Area	Conectivity	History D	History I	Heat	pH	Multif.	
Functional groups	ND	0.25 -	0.57 -	**0.98 -**	0.25 -	0.25 -	0.22 +	0.22 +	**0.99 +**	0.36
	GT	0.62 +	**0.95 +**	**1 +**	0.19 +	0.19 +	0.3 +	0.8 -	**1 -**	0.66
	WD	0.23 -	0.23 +	0.29 +	0.13 +	0.13 +	0.46 -	0.34 +	0.6 -	0.001
	AD	0.52 -	0.38 -	0.25 +	0.09 +	0.09 +	0.36 -	0.25 -	0.41 +	0.02
	LS	0.36 +	0.31 +	0.27 -	0.12 -	0.12 -	0.51 +	0.24 -	0.23 +	0.05
Taxonomic diversity	Richness	0.62 +	0.39 -	0.35 -	0.07 +	0.07 -	**0.86 -**	0.29 +	0.26 +	0.08
	Turnover	0.22 -	0.24 +	**0.87 -**	0.17 -	0.17 +	0.52 -	0.7 +	0.39 -	0.16
	Nestedness	0.75 +	0.27 -	0.55 +	0.21 +	0.21 +	0.27 +	0.34 -	0.24 -	0.06
	RRD	0.73 +	0.3 -	0.23 +	0.2 +	0.2 +	**0.87 -**	0.24 +	0.24 -	0.11
	LCBD	0.23 -	0.41 +	**1 +**	0.14 +	0.14 +	0.22 -	0.22 +	**0.87 -**	0.37
	SES	0.24 -	0.56 +	0.24 +	0.13 +	0.13 +	0.32 +	0.25 -	0.79 +	0.03
Community structure	Axis1 DCA	0.44 +	**0.96 +**	**1 +**	0.08 +	0.08 -	0.23 +	**0.99 -**	**1 -**	0.69
	Axis2 DCA	0.22 -	0.29 +	0.33 +	0.5 +	0.5 +	0.4 -	0.41 +	0.41 +	0.07

the total species, we identified 15 nutrient-demanding species. The number of these species per plot ranged between 1 and 7 and the ND value ranged between 0.004 and 0.78. The used variables explained a relatively high percentage of ND variability (R^2=0.36), reaching higher values in plots with low remnant connectivity and high soil multifunctionality (Table 2 and Fig. 2). Seed characteristics of the different species defined 17 wind-dispersed species, 11 animal-dispersed species and 54 species without specialized dispersal structures. WD, AD and LS could not be explained satisfactorily by the explanatory variables selected in this study (R^2 = 0.001, 0.02 and 0.05, respectively; Table 2).

Mean species richness per plot was 21.02, ranging from 12 to 34 species. The variability of species richness explained in the study was low (R^2 = 0.08), although there were significantly more species in plots with less soil heat load. Moreover, the distance from the plot to
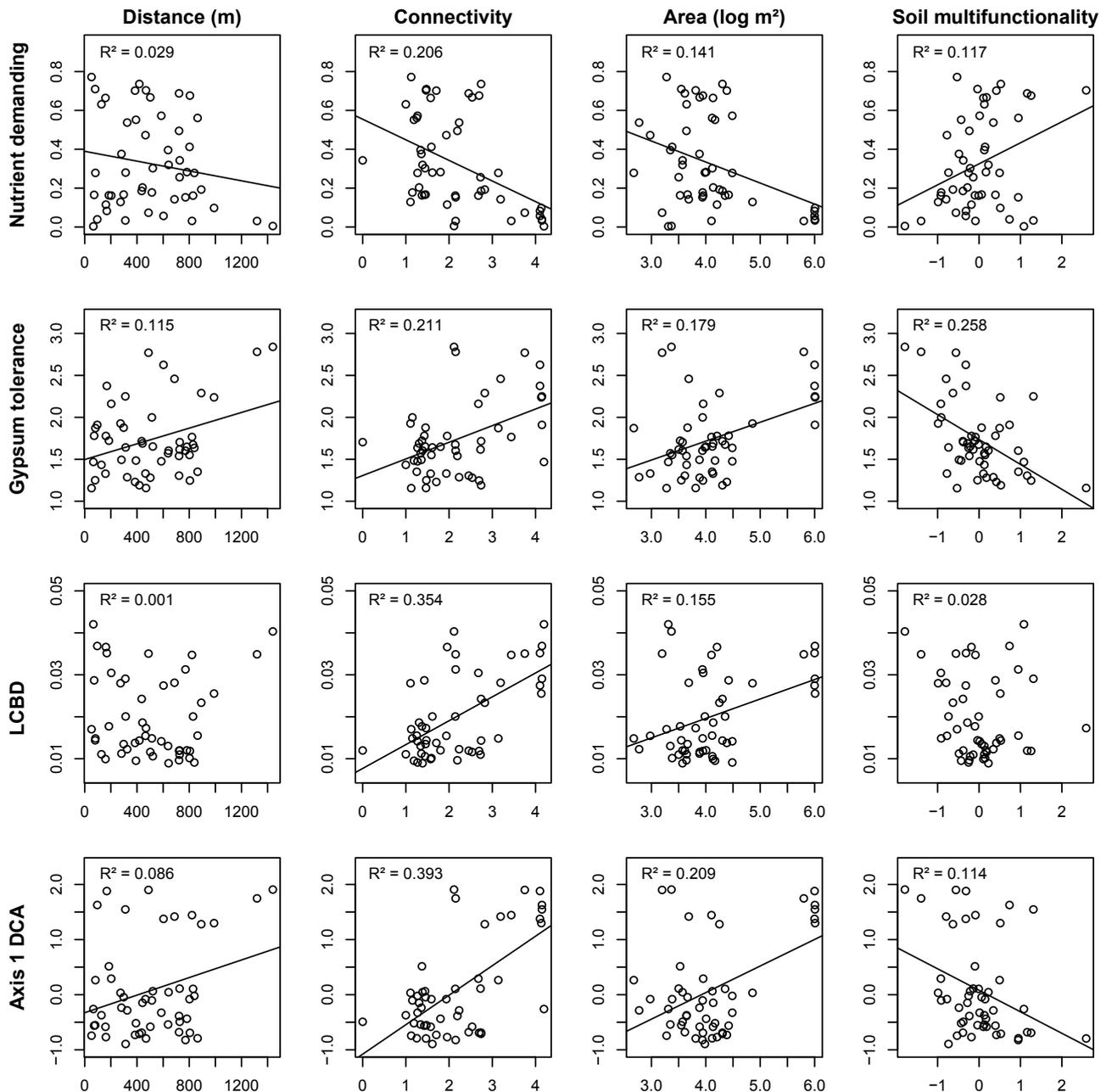
Figure 2. Relationship between some community response variables (rows) and the most important predictor (columns) detected by MMI (see Table 2). Nutrient demanding and gypsum tolerance are, respectively, the community weighted mean for nutrient-demanding species and the community weighted mean for the average gypsum tolerance; LCBD is the local contribution to beta diversity, and DCA1 is the scores in the first axis of a DCA. The predictors represent the distance to the road, connectivity and area of the patch and the index of soil multifuncionality. The regression line has been included only in the cases of significant relationship (p < 0.05).

the motorway was the second variable in importance (W_x=0.62; Table 2), but the range of variation of the estimator overlaps the 0 (Table S6). In the case of the components of within plot beta diversity (i.e. turnover and nestedness), the explained variance was also low (R^2 = 0.16 and 0.06, respectively; Table 2). Connectivity and pH (for turnover) and distance to motorway (for nestedness) showed relatively high importance

(W_x=0.87, W_x=0.7 and W_x=0.75, respectively; Table 2). However, only connectivity presented an estimator that did not overlap with 0 (Table S7 and S8). By contrast, the local contribution of each plot to landscape beta diversity (LCBD) showed a relatively higher explained variance (R^2 = 0.37), being the plots of the more connected remnants and the plots with less soil multifunctionality which had more LCBD (Fig. 2). Finally, RRD showed similar results that for species richness: the saturated model explained a low proportion of the variance (R^2 = 0.11) and only soil heat load and, to a lesser extend, distance to the road were selected as important predictors (see Table 2).

Finally, the analysis of structural characteristics of the community pointed to two different results. On one hand, in most of the cases (39 plots) the co-occurrence analysis (SES) showed patterns not significantly different from those obtained by random. Only in one plot we detected an aggregated pattern and in 10 plots a segregate pattern. Moreover, SES had an explained variance very low (R^2 =0.03) and only the soil multifunctionality had high importance (W_x=0.79), noting that plot with more soil multifunctionality showed species with segregated patterns. However, the range of variation of the estimator was overlapped with 0 (Table S11). On the other hand, the first floristic axis of the DCA had the highest explained variance (R^2 =0.69), correlating its most positive values with two variables at the landscape scale (i.e. area and connectivity) and its most negative values with the two soil variables (i.e. pH and soil multifunctionality; Table 2 and Fig. 2). This first axis of the DCA differentiated a gradient characterized by species of very different ecological behaviour (Table 3). Most of the characteristic species of the positive end were strict gypsophiles (e.g., *Arenaria cavanillesiana*, *Thymus lacaitae*, *Centaurea hyssopifolia* or *Koeleria castellana*), while those of the negative end corresponded to a mixture of species of varied ecology: typical of calcareous schrublands (*Genista scorpius*, *Lavandula latifolia*), dry grasslands (*Stipa barbata*, *S. parviflora*, *Ononis spinosa*), or ruderal habitats (*Centaurea aspera*).

Table 3. Main species associated to the first axis of the DCA.

Species	Axe 1 Negative values
Genista scorpius	-2.285
Teucrium pseudochamaepitys	-2.285
Ononis spinosa	-2.209
Ophrys speculum	-1.924
Retama sphaerocarpa	-1.924
Stipa atlantica	-1.886
Stipa parviflora	-1.886
Helianthemum marifolium	-1.886
Lavandula latifolia	-1.886
Dactylis glomerata	-1.882
Ornithogalum narbonense	-1.878
Ononis tridentata	-1.859
Phlomis lychnitis	-1.845
Centaurea aspera	-1.675
Stipa barbata	- 1.625

Species	Axe 1 Positive values
Andryala ragusina	3.062
Arenaria cavanillesiana	2.739
Frankenia thymifolia	2.709
Thymus lacaitae	2.626
Centaurea hyssopifolia	2.392
Koeleria castellana	2.378
Teucrium pumilum	2.336
Bupleurum fruticescens	2.336
Helianthemum cinereum	2.336
Linum suffruticosum	2.336
Herniaria fruticosa	2.308
Aristolochia pistolochia	2.226
Thymus vulgaris	2.226
Gypsophila bermejoi	2.198
Teucrium capitatum	2.142

DISCUSSION

The main goal of this study was to analyze jointly the effects the site characteristics, the remnants variability and the possible effects produced by a motorway on

some community features such as functional groups, taxonomic diversity and community structure (i.e. species co-occurrence index and floristic composition) in a fragmented territory with a high ecological value. The results indicate that the functional groups related to edaphic specializations (i.e. gypsum tolerance and nutrient demanding species) have been well explained, but surprisingly not only by soil predictors, but also by the landscape-scale variables. By contrast, functional groups for dispersion syndrome could not be explained by the considered variables. Moreover, the LCBD (landscape-scale structural diversity index) has been well explained, taking into account variables recorded at different scales (soil characteristics and connectivity). Finally, the first axis of the analysis of floristic composition had similar behaviour as the gypsum tolerance, being the response variables best explained in our study. In summary, our multi model inference approach suggests that the studied perennial community has a multi-scale response, since the four variables better explained have important predictors in the two scales analyzed. However, we have not found a significant effect of the distance to the road.

Important predictors

It is known that soil abiotic filters, such as, nutrient availability, pH and soil moisture are strongly related to plant species occurrence and to community assemblage (Hillerislambers et al. 2012; Kimberley et al. 2014). These soil filters have special relevance to plant communities living in habitats associated to especial soils, such as gypsum areas (Luzuriaga et al. 2012; Escudero et al. 2014). In our study, the main edaphic predictor has been the soil multifunctionality, affecting the soil specialists (nutrient demanding species and gypsum tolerance), the LCBD and the floristic composition (axis 1 of DCA). Soil multifunctionality is determinant of the functioning of ecosystems (Reiss et al. 2009; Jax 2010; Maestre et al. 2012). Greater soil multifunctionality indicates more nutrients and enzymes in the soil (slow

and rapid variables, respectively: sensu Reynolds et al. 2007) explaining the positive relationship we have found between this variable and cover of nutrient-demanding species. By contrast, the negative relationship found between gypsum tolerance and soil multifunctionality is supported by the fact that the specialist gypsum vegetation has evolved on nutrient-poor soils, as they are gypsum soils (Escudero et al. 2014). In addition to the response of soil specialists, the floristic composition as a whole shows a gradient between two contrasting situations: communities defined by high gypsum tolerance species on nutrients poor soils and communities dominated by non-specialist species on plots with greater amount of nutrients in the soil.

Moreover, gypsum habitats are drylands (Escudero et al. 2014), and therefore we expected that soil moisture should be critical to determine the community assembly. We have estimated soil moisture through the Soil Heat Load (McCune & Keon 2002). Being in a territory with relatively homogeneous soil conditions, the more soil heat load, the less moisture. This predictor has only been important for species richness and for restricted-range diversity. This is because the whole community is adapted to the extreme dry conditions of these dryland, but in the plots where the warming is lower, this abiotic filter is less strong and therefore, species richness increase by the incorporation of species less resistant to dry conditions. The effect on restricted-range diversity shows that these species are rare in this study area. Moreover, the abundance of these less adapted species is low, since the soil heat load does not affect any other variable studied.

In addition to soil variables, the effects of landscape-scale variables on the perennial community in fragmented landscape have been extensively studied, demonstrating the importance of remnants size, connectivity and historical constraints, among others (Turner 1996; Harrison 1999; Bruun 2000; Debinski & Holt 2000). Island biogeography theory (MacArthur & Wilson 1967) provided the conceptual basis to measure

the ecological impacts of habitat fragmentation (Laurance 2009). Habitat island is a discrete patch of habitat (in our study: gypsum remnants) surrounded by a matrix (in our study: agricultural fields) of contrasting unsuitable habitats (Santos et al. 2016). In many studies of island biogeography there is broad consensus that much of the variation in species diversity is explained by island size (MacArthur & Wilson 1967; Kreft et al. 2008; Nakamura et al. 2015; Santos et al. 2016). According to classic studies and studies of species-area relationships (Rosenzweig 1995), species richness increases with the patch area, although some studies put in doubt this axiom (Debinski & Holt 2000). In our study we find no relation between the area and the structural diversity indices analysed, including species richness. Two reasons can be invoked. On one hand, we do not evaluate the species richness in the whole remnant, but in plots that always have equal size. This may not reflect the differences in total species richness at the whole patch scale (Ross et al. 2002). On the other hand, the area can be a surrogate to many variables that may interact and influence species richness and diversity, such as habitat complexity and resource availability (Connor & McCoy 1979; Saunders et al. 1991; Santos et al. 2016). Consequently, the species-area relationship may depend on the degree of multicolinearity between area and these subjacent variables (Boecklen & Gotelli 1984). Our results seem to support this hypothesis, since in the larger remnants we find more gypsum specialists, which sugests that there is a positive relation between patch area and their habitat quality for some species.

Island biogeography theory focuses not only on the size of the island or habitat islands, but also on their isolation and connectivity (MacArthur & Wilson 1967; Kadmon & Pulliam 1993). In fact, in many studies it has been argued that isolation, or connectivity, is even more important than islands size to describe plant community (Saunders et al. 1991; Piessens et al. 2005; Brückmann et al. 2010). This greater importance of connectivity over patch area has also been found in

our study, since connectivity is our main predictor of landscape scale, being related to five studied variables: both soil specialists (nutrient-demanding species and gypsum tolerance), pattern of beta diversity caused by species turnover, the LCBD and the floristic composition (axis 1 of DCA). Nevertheless and surprisingly, we hypothesized an effect the connectivity on species richness due to that a highly connected patch is expected to have comparatively more species because the rescue effect (Brown & Kodric-Brown 1977) reduces extinction rates and compensates habitat loss (Lindborg & Eriksson 2004; Piessens et al. 2004), but we have not found this effect on species richness. Moreover, despite the fact that connectivity is largely related to the dispersal capacities of a species or community (Piessens et al. 2005), we also have not found any effect of the connectivity in the response of any dispersal traits analyzed (wind-dispersal, animal-dispersal and without specialized dispersal structures). This may be due to the fact that we have assigned the most probable dispersion for each species, but we not take into account that each propagule can often be dispersed in a variety of ways (Higgins et al. 2003). It may also be due to the distances between patches are not in the range that can affect the different forms of dispersion, either because this range is very high (maybe for species lacking of specialized dispersal structures) or because it is very low (maybe for wind and animal-dispersal). As already mentioned, connectivity has consequences on several of the studied variables. Firstly, connectivity has affected the distribution of soil specialist plant species. Gypsum tolerance is higher in plots with higher connectivity. One possible explanation is that this community is especially affected from the isolation and lack of genetic exchange between more isolated patch (Pueyo & Alados 2007; Pueyo et al. 2008; Matesanz et al. 2015), which would lead to the disappearance of some species. On the other hand, it is possible that the most connected remnants are in turn the less degraded patches, and therefore, have better conditions to maintain these

habitat specialists. By contrast, nutrient-demanding species reaches higher values in the less connected plots, and therefore these plots have more soil nutrients. In nutrient-poor soils, such as gypsum soils of this study area, these nutrients have to come from human disturbance. In agroecosystems, remnants can receive nutrients from the cultivated matrix (Pueyo et al. 2008) and from grazing by sheep that leave their droppings. Therefore, in our study area, the less connected patches have more disturbances. Secondly, we found that patches more connected showed more LCBD than isolated ones. This could be due to the fact that the higher values of LCBD indicate that there are greater cover of less abundant species, although no more rare species, since Restricted-Range Diversity do not show the same response. Finally, as expected due to the great importance of connectivity and isolation in the composition of many communities (Kadmon & Pulliam 1993), we have found that connectivity is one of the most important factors in defining the first axis of the DCA.

In addition to the current area or connectivity of a remnant, some studies have described that the historic constraints are determinant to understand many descriptors of present-day plant communities, effecting on richness, diversity, composition and function (Lindborg & Eriksson 2004; Brudvig & Damschen 2011; Ewers et al. 2013; Del Castillo 2015; Jakobsson et al. 2016). However, we have not found any effect of the analysed historic variable in our study, perhaps because in the considered time the changes have not been very intense.

We have included the distance to a motorway as a landscape variable with possible effects on surrounding plant communities (Tikka et al. 2000; Lugo & Gucinski 2000; Tikka et al. 2001; Arenas et al. 2015; Jakobsson et al. 2016; Arenas et al. 2017). These effects are based on the capacity of road verges to channel parallel and transverse flows to the road (Tikka et al. 2001; Bochet et al. 2007; de la Riva et al. 2011; Smit & Asner 2012; von der Lippe et al. 2013; Auffret & Cousins 2013; Coulson et al. 2013; Arenas et al. 2017). Considering these and other

studies we hypothesize the existence of some effects between distance to the motorway and the variables analyzed (Table 1). Among the analyzed variables, we found weak signs of possible effects on four of them: gypsum tolerance, species richness, nestedness and restricted-range diversity (> 60% of relative importance). However, in none of the four variables the effect is clear, since the confidence intervals to the model-averaged parameter estimates overlaps with 0. This absence of effects may be due to that none of these response variables, except gypsum tolerance, have been able to be effectively modelled (low R^2 value), which seems to indicate that other non-sampled factors may be more determinants of their variation. On the other hand, it is possible that the effects associated to the road are manifested only at a very short distance (few meters) and therefore have been diluted in the range of distances studied here. In that case, more detailed studies would be needed to highlight this effect.

Overview of the community

The best-modelled response variable in this study is the floristic composition defined by the first axis of the DCA ($R^2 = 0.69$), followed by gypsum tolerance ($R^2 = 0.66$). Moreover, both variables are described practically by the same predictors, same relative importance and sign. These results suggest that gypsum plant community analyzed seems to have a multiscale response, determined by soil specialists and the degree of disturbance. The first axis of DCA describes a gradient from typical gypsophile vegetation to more degraded (grassland and nitrophilous species) areas. Both natural and degraded communities are responding to descriptors acting at two scales: local one, associated to soil characteristics and landscape, conditioned by patch area and connectivity. As we have shown above, in gypsum soils the greater amount of nutrients is associated to disturbances and soil uses for agricultural (Pueyo et al. 2008) and livestock activities. We have also argued previously that, in our study area, the less connected patches have more disturbances.

In relation to patch area, Saunder et al. (1991) pointed out that in small remnants, ecosystem dynamics are probably driven predominantly by external perturbations associated with the edges, while larger remnants have a bigger core area that is unaffected by the environmental and biotic changes associated to edge effects. Therefore, we again point out to the idea that the area, being a landscape-scale variable, possibly acts as a surrogate of other variables at the local level. So, area and connectivity are defining habitat quality, more than carrying capacity, extinction debt or rescue effect. Therefore, although our multi model inference approach suggests that the studied perennial community has a multiscale response, the local scale and microsite scale have more weight on community configuration.

Conclusions for management, conservation and ecological restoration of gypsum ecosystems in fragmented landscape

Gypsum habitats have historically been perceived as badlands with no special conservation interest (Escudero et al. 2014). But in the last decades, due to their rarity and singularity, they have begun to be protected by regional and goverments (Moreno 2008), as well as by the European Union (Directive 92/43/CEE, 1992). However, the effect of global change drivers, such as landscape fragmentation and human-driven degradation is still significant in these gypsum areas (Matesanz et al. 2010). In addition, gypsum species are more affected by habitat fragmentation than generalist species (Pueyo et al. 2008).

From the results of this study we can derive conclusions for the management, conservation and ecological restoration of these fragmented gypsum ecosystems. Gypsum plant communities are organized mainly according to the soil variables, and even, the landscape scale predictors are ultimately also affecting on soil quality. Therefore, in order to their conservation, the core zone of the remnants should be protected as much as possible, limiting the activities that degrade

the soil and trying to reduce as much as possible the edge effect of remnants. In the same line, to propose the ecological restoration of degraded fragments, the efforts should focus on the recovery of the characteristics of gypsum soils.

In fragmented landscapes Del Castillo (2015) pointed out that beta diversity among patch (in our study: LCBD and RRD) is an essential element for ecosystem functioning and resilience compared with the traditional perspective that emphasizes within-patch diversity (in our study: Richness, Turnover and Nestedness indices). LCBD has been the structural diversity variable best explained, with connectivity being its main predictor, followed by soil quality. So, management and ecological restoration measures must maintain and increase the connectivity of remnants. But management measures must take into account the soil characteristics, not only because nutrients soil have been an important descriptor of LCBD, but also because the community of gypsum plants is highly dependent on soil characteristics, as we have described throughout this study and other authors have also pointed out (Pueyo et al. 2008; Escudero et al. 2014). The enhancement of connectivity can be achieved by ecological restoration of abandoned fields, making special emphasis on restoring soil conditions. In addition, in areas crossed by roads and motorways, such as our study, road verges can be used for this purpose, as long as its management contributes to conservation of interesting plant communities. For example, in chapter 4 of this thesis we have shown that roadcuts are capable of housing an interesting community of gypsophiles, even without proper managements. However, in order to use these novel habitats in improving connectivity, more research is necessary.

Conclusions for motorway effects: further research needed

Our study area is crossed by a motorway. We have hypothesized that this motorway, and more specifically the distance to it, could have positive effects on plant

community studied. However, we have not found such effects. Nevertheless, further research is necessary to really discern the effect that roads and motorways could have, since there is a lot of solid-based literature pointing to possible effects (Tikka et al. 2000; Lugo & Gucinski 2000; Tikka et al. 2001; Arenas et al. 2015; Jakobsson et al. 2016; Arenas et al. 2017).

In our study it is possible that we have not found any effect for several reasons, a critical view of them allows us to give some recommendations for these necessary future investigations: 1) As we have previously mentioned, it is possible that the effects associated to the road are manifested only at a very short distance (few meters) and therefore have been diluted in the range of distances studied here. Future research should first be focused on the direct study of these flows, mainly flows from road verges to surrounding areas, since it is the least studied. 2) Many research, including this one, analyze the road verges from the vision of provision of any ecosystem services, however the management of these sites is never done for that purpose. We propose the need for future research to be raised from long-term management in order to make easier to find the possible positive effects hypothesized in many studies.

ACKNOWLEDGEMENTS

REFERENCES

Anacker, B.L. 2014. The nature of serpentine endemism. American journal of botany 101: 219–224.

Anderson, J., & Ingram, J. 1989. Tropical soil biology and fertility: A handbook of methods. CAB International, Wallingford, Oxon, UK.

Arenas, J.M., Escudero, A., Magro, S., Balaguer, L., & Casado, M.A. 2015. Woody colonization of road embankments: A large spatial scale survey in central Spain. Landscape and Urban Planning 141: 52–58.

Arenas, J.M., Lázaro-Lobo, A., Mola, I., Escudero, A., & Casado, M.A. 2017. The influence of site factors and proximity of adjacent vegetation on tree regeneration into roadslopes. Ecological Engineering 101: 120–129.

Auffret, A.G., & Cousins, S.A.O. 2013. Grassland connectivity by motor vehicles and grazing livestock. Ecography 001–008.

Baselga, A. 2010. Partitioning the turnover and nestedness components of beta diversity. Global Ecology and Biogeography 19: 134–143.

Bochet, E., García-Fayos, P., & Tormo, J. 2007. Road slope revegetation in semiarid Mediterranean environments. Part I: seed dispersal and spontaneous colonization. Restoration Ecology 15: 88–96.

Boecklen, W.J., & Gotelli, N.J. 1984. Island biogeographic theory and conservation practice: Species-area or specious-area relationships? Biological Conservation 29: 63–80.

Brauner, N., & Shacham, M. 1998. Role of range and precision of the independent variable in regression of data. AIChE Journal 44: 603–611.

Brooks, R.R. 1987. Serpentine and its vegetation: a multidisciplinary approach. Dioscorides Press, Portland.

Brown, J.H., & Kodric-Brown, A. 1977. Turnover Rates in Insular Biogeography: Effect of Immigration on Extinction. Ecology 58: 445–449.

Brückmann, S. V., Krauss, J., & Steffan-Dewenter, I. 2010. Butterfly and plant specialists suffer from reduced connectivity in fragmented landscapes. Journal of Applied Ecology 47: 799–809.

Brudvig, L.A., & Damschen, E.I. 2011. Land-use history, historical connectivity, and land management interact to determine longleaf pine woodland understory richness and composition. Ecography 34: 257–266.

Bruun, H.H. 2000. Patterns of species richness in dry grassland patches in an agricultural landscape. Ecography 23: 641–650.

Burnham, K.P., & Anderson, D.R. 2002. Model Selection and Multimodel Inference. A Practical Information-Theoretical Approach. Springer-Verlag, New York.

Calcagno, V. 2013. glmulti: Model selection and multimodel inference made easy.

Del Castillo, R.F. 2015. A conceptual framework to describe the ecology of fragmented landscapes and implications for conservation and management. Ecological Applications 25: 1447–1455.

Castroviejo, S. 2016. Flora ibérica. Real Jardín Botánico, CISC, Madrid.

Chen, Y. 2012. MBI: (M)ultiple-site (B)iodiversity (I)ndices Calculator.

Coffin, A.W. 2007. From roadkill to road ecology: A review of the ecological effects of roads. Journal of Transport Geography 15: 396–406.

Connor, E.F., & McCoy, E.D. 1979. The Statistics and Biology of the Species-Area Relationship. The American Naturalist 113: 791–833.

Coulson, C., Spooner, P.G., Lunt, I.D., & Watson, S.J. 2013. From the matrix to roadsides and beyond: the role of isolated paddock trees as dispersal points for invasion (J. Diez, Ed.). Diversity and Distributions. doi: 10.1111/ddi.12135

Debinski, D.M., & Holt, R.D. 2000. A survey and overview of habitat fragmentation experiments. Conservation Biology 14: 342–355.

Diamond, J.M. 1975. Assembly of species communities. In Cody, M.L. & Diamond, J. (eds.), Ecology and evolution of communities, pp. 342–444. Harvard University Press, Cambridge, Massachusetts and London.

Eivazi, F., & Tabatabai, M. 1988. Glucosidases and galactosidases in soils. Soil Biology and Biochemistry 20: 601–606.

Escudero, A., Palacio, S., Maestre, F.T., & Luzuriaga, A.L. 2014. Plant life on gypsum: a review of its multiple facets. Biological rewiews 90: 1–18.

Ewers, R.M., Didham, R.K., Pearse, W.D., Lefebvre, V., Rosa, I.M.D., Carreiras, J.M.B., Lucas, R.M., & Reuman, D.C. 2013. Using landscape history to predict biodiversity patterns in fragmented landscapes (M. Bonsall, Ed.). Ecology Letters 16: 1221–1233.

Fahrig, L. 2013. Rethinking patch size and isolation effects: The habitat amount hypothesis. Journal of Biogeography 40: 1649–1663.

Forman, R.T.T. 2000. Estimate of the Area Affected Ecologically by the Road System in the United States. Conservation Biology 14: 31–35.

Forman, R.T.T., & Alexander, L.E. 1998. Road and their major ecological effects. Annual Review of Ecology and Systematics 29: 207–231.

Frenkel, R. 1970. Ruderal vegetation along some californian roadsides. Berkeley.

Fu, W., Liu, S., Degloria, S.D., Dong, S., & Beazley, R. 2010. Characterizing the "fragmentation–barrier" effect of road networks on landscape connectivity: A case study in Xishuangbanna, Southwest China. Landscape and Urban Planning 95: 122–129.

Geho, E.M., Campbell, D., & Keddy, P.A. 2007. Quantifying ecological filters: The relative impact of herbivory, neighbours, and sediment on an oligohaline marsh. Oikos 116: 1006–1016.

Gotelli, N.J. 2000. Null model analysis of species co-occurrence patterns. Ecology 81: 2606–2621.

Gotelli, N., Hart, E., & Ellison, A. 2015. Package " EcoSimR ." R package

Grashof-Bokdam, C. 1997. Forest species in an agricultural landscape in the Netherlands: Effects of habitat fragmentation. Journal of Vegetation Science 8: 21–28.

Harrison, S. 1999. Local and regional diversity in a patchy landscape: Native, alien, and endemic herbs on serpentine. Ecology 80: 70–80.

Higgins, S.I., Nathan, R., & Cain, M.L. 2003. Are Long-Distance Dispersal Events in Plants Usually Caused By Nonstandard Means of Dispersal? Ecology 84: 1945–1956.

Hillerislambers, J., Adler, P.B., Harpole, W.S., Levine, J.M., & Mayfield, M.M. 2012. Rethinking Community Assembly through the Lens of Coexistence Theory. Annu. Rev. Ecol. Evol. Syst 43: 227–48.

Honnay, O., Verheyen, K., Butaye, J., Jacquemyn, H., Bossuyt, B., & Hermy, M. 2002. Possible effects of habitat fragmentation and climate change on the range of forest plant species. Ecology Letters 5: 525–530.

Jakobsson, S., Fukamachi, K., & Cousins, S.A.O. 2016. Connectivity and management enables fast recovery of plant diversity in new linear grassland elements. Journal of Vegetation Science 27: 19–28.

Jax, K. 2010. Ecosystem functioning. Cambridge University Press.

Johnston, F.M., & Johnston, S.W. 2004. Impacts of Road Disturbance on Soil Properties and on Exotic Plant Occurrence in Subalpine Areas of the Australian Alps. Arctic, Antarctic, and Alpine Research 36: 201–207.

Kadmon, R., & Pulliam, H.R. 1993. Island biogeography: effects of geographical isolation on species composition. Ecology 74: 977–981.

Keddy, P.A. 1992. Assembly and Response Rules: Two Goals for Predictive Community Ecology. Journal of Vegetation Science 3: 157–164.

Kershaw, M., Williams, P., & Mace, G. 1994. Conservation of Afrotropical antelopes: consequences and efficiency of using different site selection methods and diversity criteria. Biodiversity & Conservation 3: 354–372.

Kimberley, A., Alan Blackburn, G., Duncan Whyatt, J., & Smart, S.M. 2014. Traits of plant communities in fragmented forests: The relative influence of habitat spatial configuration and local abiotic conditions. Journal of Ecology 102: 632–640.

Kreft, H., Jetz, W., Mutke, J., Kier, G., & Barthlott, W. 2008. Global diversity of island floras from a macroecological perspective. Ecology Letters 11: 116–127.

de la Riva, E.G., Casado, M.A., Jiménez, M.D., Mola, I., Costa-Tenorio, M., & Balaguer, L. 2011. Rates of local colonization and extinction reveal different plant community assembly mechanisms on road verges in central Spain. Journal of Vegetation Science. 22: 292–302.

Laurance, W.F. 2009. Beyond island biogeography theory. Understanding habitat fragmentation in the real world. In Losos, J.B. & Ricklefs, R.E. (eds.), The theory of island biogeography

revisited, pp. 214–236. Princeton University Press, Princeton, New Jersey.

Legendre, P., & De Cáceres, M. 2013. Beta diversity as the variance of community data: Dissimilarity coefficients and partitioning. Ecology Letters 16: 951–963.

Lindborg, R., & Eriksson, O. 2004. Historical landscape connectivity affects present plant species diversity. Ecology 85: 1840–1845.

Lindenmayer, D.B., & Fischer, J. 2007. Tackling the habitat fragmentation panchreston. Trends in ecology & evolution 22: 127–32.

von der Lippe, M., Bullock, J.M., Kowarik, I., Knopp, T., & Wichmann, M. 2013. Human-mediated dispersal of seeds by the airflow of vehicles. PloS one 8: e52733.

López-Martínez, J.O., Hernández-Stefanoni, J.L., Dupuy, J.M., & Meave, J.A. 2013. Partitioning the variation of woody plant b-diversity in a landscape of secondary tropical dry forests across spatial scales. Journal of Vegetation Science 24: 33–45.

Lugo, A.E., & Gucinski, H. 2000. Function, effects, and management of forest roads. Forest Ecology and Management 133: 249–262.

Luzuriaga, A.L., Sánchez, A.M., Maestre, F.T., & Escudero, A. 2012. Assemblage of a semi-arid annual plant community: abiotic and biotic filters act hierarchically. PloS one 7: e41270.

MacArthur, R.H., & Wilson, E.O. 1967. The Theory of Island Biogeography. Princeton University Press, Princeton.

Maestre, F.T., Quero, J.L., Gotelli, N.J., Escudero, A., Ochoa, V., Delgado-Baquerizo, M., García-Gómez, M., Bowker, M.A., Soliveres, S., Escolar, C., García-Palacios, P., Berdugo, M., Valencia, E., Gozalo, B., Gallardo, A., Aguilera, L., Arredondo, T., Blones, J., Boeken, B., Bran, D., Conceição, A. a, Cabrera, O., Chaieb, M., Derak, M., Eldridge, D.J., Espinosa, C.I., Florentino, A., Gaitán, J., Gatica, M.G., Ghiloufi, W., Gómez-González, S., Gutiérrez, J.R., Hernández, R.M., Huang, X., Huber-Sannwald, E., Jankju, M., Miriti, M., Monerris, J., Mau, R.L., Morici, E., Naseri, K., Ospina, A., Polo, V., Prina, A., Pucheta, E., Ramírez-Collantes, D. a, Romão, R., Tighe, M., Torres-Díaz, C., Val, J., Veiga, J.P., Wang, D., & Zaady, E. 2012. Plant species richness and ecosystem multifunctionality in global drylands. Science 335: 214–8.

Matesanz, S., Gianoli, E., & Valladares, F. 2010. Global change and the evolution of phenotypic plasticity in plants. In Year in Evolutionary Biology, pp. 35–55.

Matesanz, S., Gómez-Fernández, A., Alcocer, I., & Escudero, A. 2015. Fragment size does not matter when you are well connected: Effects of fragmentation on fitness of coexisting gypsophiles. Plant Biology 17: 1047–1056.

Maurer, K., Durka, W., & Stocklin, J. 2003. Frequency of plant species in remnants of calcareous grassland and their dispersal and persistence characteristics. Basic and Applied Ecology 4: 307–316.

McCune, B., & Keon, D. 2002. Equations for potential annual direct incident radiation and heat load. Journal of Vegetation Science

13: 603–606.

Moreno, J.C. 2008. Lista Roja de la Flora Vascular Española. Dirección General de Medio Natural y Política Forestal Ministerio de Medio Ambiente y Medio rural y Marino Y Sociedad Española de Biología de la Conservación de Plantas, Madrid, España.

Mota, J.F., Gomez, P.S., Merlo Calvente, M.E., Catalan Rodriguez, P., Lumbreras, E.L., de La Cruz Rot, M., Navarro Reyes, F.B., Gallardo, F.M., Esteban, C.B., Martinez Labarga, J.M., Ollero, H.S., Tendero, F.V., Laliga, L.S., Hernandez, F.M., Garrido Becerra, J.A., & Perez Garcia, F.J. 2009. Aproximación a la checklist de los gipsófitos ibéricos. Anales de Biologia 31: 71–80.

Myers, J.A., Chase, J.M., Jiménez, I., Jørgensen, P.M., Araujo-Murakami, A., Paniagua-Zambrana, N., & Seidel, R. 2013. Beta-diversity in temperate and tropical forests reflects dissimilar mechanisms of community assembly. Ecology Letters 16: 151–157.

Nakamura, A., Burwell, C.J., Lambkin, C.L., Katabuchi, M., Mcdougall, A., Raven, R.J., & Neldner, V.J. 2015. The role of human disturbance in island biogeography of arthropods and plants: An information theoretic approach. Journal of Biogeography 42: 1406–1417.

National Geographic Institute of Spain. 2011. PNOA, Plan Nacional de Ortofotografía Aérea.

Ninyerola, M., Pons, X., & Roure, J. 2005. Atlas Climático Digital de la Península Ibérica. Metodología y aplicaciones en bioclimatología y geobotánica. Universidad Autónoma de Barcelona, Bellaterra.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., & Wagner, H. 2015. vegan: Community Ecology Package.

Piessens, K., Honnay, O., & Hermy, M. 2005. The role of fragment area and isolation in the conservation of heathland species. Biological Conservation 122: 61–69.

Piessens, K., Honnay, O., Nackaerts, K., & Hermy, M. 2004. Plant species richness and composition of heathland relics in north-western Belgium: evidence for a rescue-effect? Journal of Biogeography 31: 1683–1692.

Pueyo, Y., & Alados, C.L. 2007. Effects of fragmentation, abiotic factors and land use on vegetation recovery in a semi-arid Mediterranean area. Basic and Applied Ecology 8: 158–170.

Pueyo, Y., Alados, C.L., Barrantes, O., Komac, B., & Rietkerk, M. 2008. Differences in gypsum plant communities associated with habitat fragmentation and livestock grazing. Ecological Applications 18: 954–964.

QGIS Development Team. 2013. QGIS Geographic Information System.

Quintana-Ascencio, P.F., & Menges, E.S. 1996. Inferring metapopulation dynamics from patch level incidence of Florida scrub plants. Conservation Biology 10: 1210–1219.

R Core Team. 2015. R: A Language and Environment for Statistical Computing.

Reiss, J., Bridle, J.R., Montoya, J.M., & Woodward, G. 2009. Emerging horizons in biodiversity and ecosystem functioning research. Trends in Ecology and Evolution 24: 505–514.

Reynolds, J.F., Smith, D.M.S., Lambin, E.F., Turner, B.L., Mortimore, M., Batterbury, S.P.J., Downing, T.E., Dowlatabadi, H., Fernández, R.J., Herrick, J.E., Huber-Sannwald, E., Jiang, H., Leemans, R., Lynam, T., Maestre, F.T., Ayarza, M., & Walker, B. 2007. Global desertification: building a science for dryland development. Science 316: 847–51.

Ricklefs, R.E. 1987. Community Diversity: Relative Roles of Local and Regional Processes. Science 235: 167–171.

Rivas-Martínez, S., Díaz, T.E., Fernandez-Gonzalez, F., Izco, J., Loidi, J., Lousã, M., & Penas, A. 2002. Vascular plant communities of Spain and Portugal: addenda to the syntaxonomical checklis of 2001. Part 1. Itinera Geobotanica 15: 5–992.

Rosenzweig, M.L. 1995. Species diversity in space and time. Cambridge University Press, New York.

Ross, K.A., Fox, B.J., & Fox, M.D. 2002. Changes to plant species richness in forest fragments: Fragment age, disturbance and fire history may be as important as area. Journal of Biogeography 29: 749–765.

Sabino-Marques, H., & Mira, A. 2011. Living on the verge: Are roads a more suitable refuge for small mammals than streams in Mediterranean pastureland? Ecological Research 26: 277–287.

Santos, A.M.C., Field, R., & Ricklefs, R.E. 2016. New directions in island biogeography. Global Ecology and Biogeography 25: 751–768.

Saunders, D. a., Hobbs, R.J., & Margules, C.R. 1991. Biological Consequences of Ecosystem Fragmentation: A Review. Conservation Biology 5: 18–32.

Smit, I.P.J., & Asner, G.P. 2012. Roads increase woody cover under varying geological, rainfall and fire regimes in African savanna. Journal of Arid Environments 80: 74–80.

Spooner, P., & Smallbone, L. 2009. Effects of road age on the structure of roadside vegetation in south-eastern Australia. Agriculture, Ecosystems & Environment 129: 57–64.

Stone, L., & Roberts, A. 1990. the Checkerboard Score and Species Distributions. Oecologia 85: 74–79.

Tabatabai, M., & Bremner, J. 1969. Use of p-nitrophenyl phosphate for assay of soil phosphatase activity. Soil biology and biochemistry 1: 301–307.

Tikka, P., Högmander, H., & Koski, P. 2001. Road and railway verges serve as dispersal corridors for grassland plants. Landscape ecology 16: 659–666.

Tikka, P., Koski, P., Kivelä, R., & Kuitunen, M. 2000. Can grassland plant communities be preserved on road and railway verges? Applied Vegetation Science 3: 25–32.

Trombulak, S.C., & Frissell, C.A. 2000. Review of ecological effects of roads on terrestrial and aquatic communities. Conservation Biology 14: 18–30.

Turner, I. 1996. Species Loss in Fragments of Tropical Rain Forest: A Review of the Evidence. The Journal of Applied Ecology 33: 200–209.

Wilson, E.O. 1989. Threats to biodiversity. Scientific American 261: 108–116.

Yeomans, J.C., & Bremner, J.M. 1988. A rapid and precise method for routine determination of organic carbon in soil. Communications in Soil Science and Plant Analysis 19: 1467–1476.

Young, A., Boyle, T., & Brown, T. 1996. The population genetic consequences of habitat fragmentation for plants. Trends in Ecology & Evolution 11: 413–418.
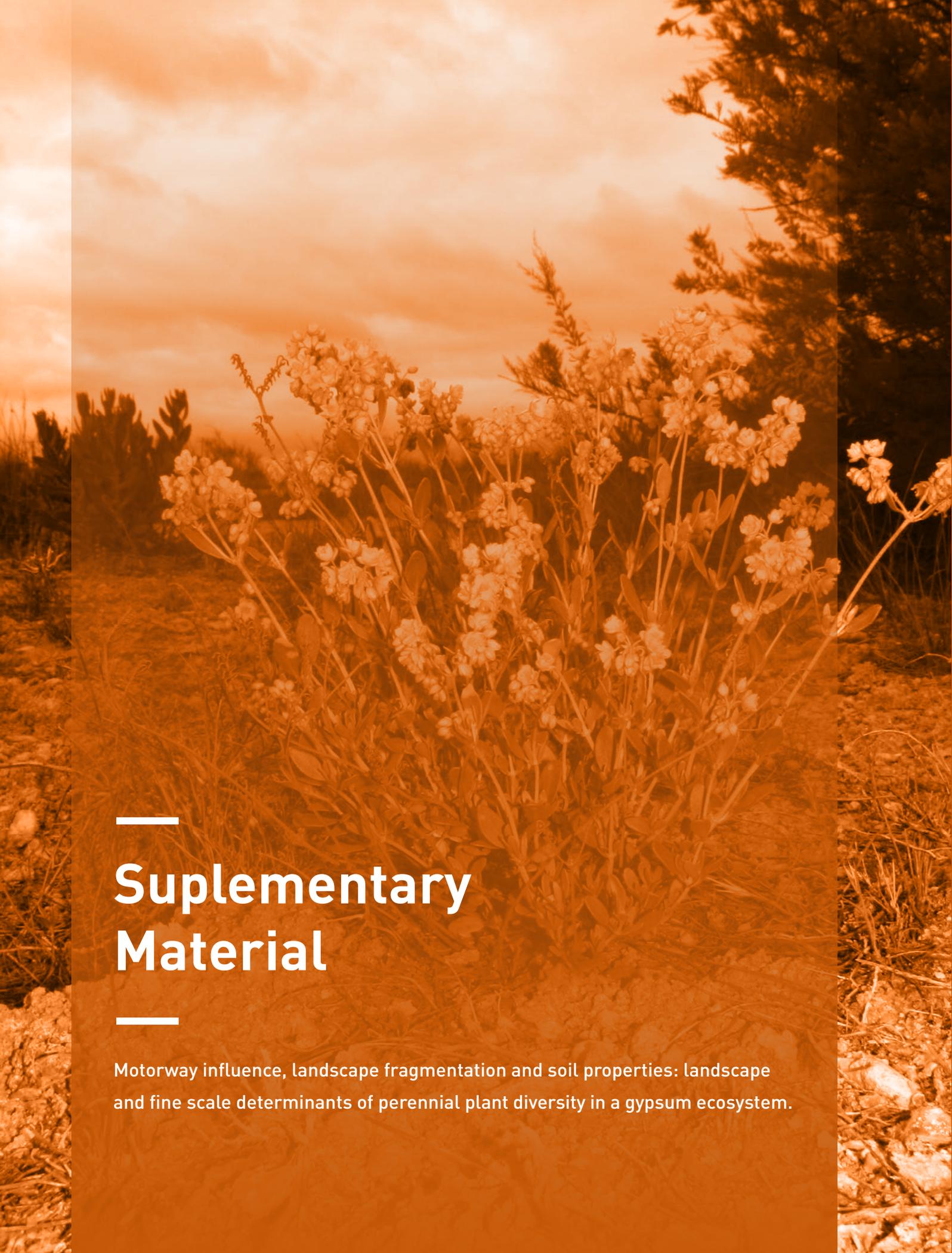
Suplementary Material

Motorway influence, landscape fragmentation and soil properties: landscape and fine scale determinants of perennial plant diversity in a gypsum ecosystem.

Supplementary results associated with the article: Arenas, J.M. et al. "*Motorway influence, landscape fragmentation and soil properties: landscape and fine scale determinants of perennial plant diversity in a gypsum ecosystem*".

Table S1. Model-averaged parameter estimates for each predictor for community weighted mean for nutrient-demanding species (ND), and the confidence intervals to these coefficients (alpha risk = 0.1). The coefficients that the confidence intervals to the model-averaged parameter estimates do not overlap with 0 have been highlighted in bold.

ND	Coefficient	Confidence interval	
Distance	-0.00001	-0.00010	0.00007
Area	-0.038	-0.112	0.036
Connectivity	**-0.106**	**-0.164**	**-0.048**
History D	-0.025	-0.117	0.066
History I	-0.017	-0.112	0.078
Soil Heat Load	0.048	-0.457	0.553
Soil pH	0.011	-0.139	0.162
Soil Multifunctionality	**0.134**	**0.069**	**0.200**

Tabla S2. Model-averaged parameter estimates for each predictor for community weighted mean for the average gypsum tolerance (GT) of the species of each plot, and the confidence intervals to these coefficients (alpha risk = 0.1). The coefficients that the confidence intervals to the model-averaged parameter estimates do not overlap with 0 have been highlighted in bold.

GT	Coefficient	Confidence interval	
Distance	0.00015	-0.00011	0.00040
Area	**0.144**	**0.038**	**0.250**
Connectivity	**0.185**	**0.106**	**0.264**
History D	0.026	-0.085	0.138
History I	0.014	-0.098	0.127
Soil Heat Load	0.234	-0.735	1.204
Soil pH	-0.467	-1.023	0.089
Soil Multifunctionality	**-0.309**	**-0.400**	**-0.218**

Tabla S3. Model-averaged parameter estimates for each predictor for community weighted mean for wind-dispersed species (WD), and the confidence intervals to these coefficients (alpha risk = 0.1). The coefficients that the confidence intervals to the model-averaged parameter estimates do not overlap with 0 have been highlighted in bold.

WD	Coefficient	Confidence interval	
Distance	0.00000	-0.00003	0.00003
Area	0.000	-0.013	0.014
Connectivity	0.003	-0.012	0.018
History D	0.003	-0.019	0.026
History I	0.004	-0.027	0.034
Soil Heat Load	-0.163	-0.578	0.251
Soil pH	0.029	-0.076	0.134
Soil Multifunctionality	-0.018	-0.052	0.015

Tabla S4. Model-averaged parameter estimates for each predictor for community weighted mean for animal-dispersed species (AD), and the confidence intervals to these coefficients (alpha risk = 0.1). The coefficients that the confidence intervals to the model-averaged parameter estimates do not overlap with 0 have been highlighted in bold.

AD	Coefficient	Confidence interval	
Distance	-0.00004	-0.00012	0.00005
Area	-0.009	-0.036	0.019
Connectivity	0.001	-0.013	0.016
History D	0.001	-0.017	0.020
History I	0.002	-0.027	0.032
Soil Heat Load	-0.119	-0.523	0.285
Soil pH	-0.012	-0.104	0.080
Soil Multifunctionality	0.011	-0.020	0.042

Tabla S5. Model-averaged parameter estimates for each predictor for community weighted mean for species lacking structures associated with specific dispersal mechanisms (LS), and the confidence intervals to these coefficients (alpha risk = 0.1). The coefficients that the confidence intervals to the model-averaged parameter estimates do not overlap with 0 have been highlighted in bold.

LS	Coefficient	Confidence interval	
Distance	0.00003	-0.00006	0.00011
Area	0.007	-0.024	0.039
Connectivity	-0.004	-0.027	0.019
History D	-0.005	-0.040	0.030
History I	-0.006	-0.055	0.044
Soil Heat Load	0.326	-0.402	1.055
Soil pH	-0.008	-0.122	0.105
Soil Multifunctionality	0.001	-0.023	0.025

Tabla S6. Model-averaged parameter estimates for each predictor for species Richness, and the confidence intervals to these coefficients (alpha risk = 0.1). The coefficients that the confidence intervals to the model-averaged parameter estimates do not overlap with 0 have been highlighted in bold.

Richness	Coefficient	Confidence interval	
Distance	0.00245	-0.00189	0.00680
Area	-0.420	-1.723	0.883
Connectivity	-0.282	-1.321	0.757
History D	0.016	-0.703	0.735
History I	-0.029	-1.145	1.086
Soil Heat Load	-29.487	-59.335	0.362
Soil pH	1.088	-4.008	6.184
Soil Multifunctionality	0.144	-0.798	1.085

Tabla S7. Model-averaged parameter estimates for each predictor for patterns of beta diversity caused by species turnover, and the confidence intervals to these coefficients (alpha risk = 0.1). The coefficients that the confidence intervals to the model-averaged parameter estimates do not overlap with 0 have been highlighted in bold.

Turnover	Coefficient	Confidence interval	
Distance	0.00000	-0.00003	0.00003
Area	0.000	-0.014	0.015
Connectivity	**-0.029**	**-0.057**	**-0.001**
History D	-0.004	-0.027	0.019
History I	0.005	-0.028	0.038
Soil Heat Load	-0.211	-0.674	0.251
Soil pH	0.106	-0.052	0.265
Soil Multifunctionality	-0.008	-0.032	0.016

Tabla S8. Model-averaged parameter estimates for each predictor for patterns of beta diversity caused by species nestedness, and the confidence intervals to these coefficients (alpha risk = 0.1). The coefficients that the confidence intervals to the model-averaged parameter estimates do not overlap with 0 have been highlighted in bold.

Nestedness	Coefficient	Confidence interval	
Distance	0.00003	-0.00001	0.00008
Area	-0.002	-0.011	0.008
Connectivity	0.006	-0.007	0.020
History D	0.005	-0.014	0.024
History I	0.003	-0.017	0.023
Soil Heat Load	0.022	-0.121	0.165
Soil pH	-0.015	-0.073	0.042
Soil Multifunctionality	-0.001	-0.010	0.007

Tabla S9. Model-averaged parameter estimates for each predictor for restricted-range diversity (RRD), and the confidence intervals to these coefficients (alpha risk = 0.1). The coefficients that the confidence intervals to the model-averaged parameter estimates do not
overlap with 0 have been highlighted in bold.

RRD	Coefficient	Confidence interval	
Distance	0.00302	-0.00119	0.00722
Area	-0.206	-1.144	0.733
Connectivity	0.022	-0.611	0.655
History D	0.400	-1.306	2.105
History I	0.204	-1.546	1.954
Soil Heat Load	**-26.992**	**-53.232**	**-0.753**
Soil pH	0.395	-3.364	4.155
Soil Multifunctionality	-0.095	-0.906	0.716

Tabla S10. Model-averaged parameter estimates for each predictor for local
contribution to beta diversity (LCBD) of each remnant, and the confidence intervals to these coefficients (alpha risk = 0.1). The coefficients that the confidence intervals to the model-averaged parameter estimates do not overlap with 0 have been highlighted in bold.

LCBD	Coefficient	Confidence interval	
Distance	0.00000	0.00000	0.00000
Area	0.001	-0.001	0.003
Connectivity	**0.006**	**0.004**	**0.008**
History D	0.000	-0.002	0.002
History I	0.001	-0.003	0.004
Soil Heat Load	-0.001	-0.021	0.018
Soil pH	0.000	-0.006	0.006
Soil Multifunctionality	**-0.003**	**-0.006**	**-0.0001**

Tabla S11. Model-averaged parameter estimates for each predictor for standardized effect size of C-score index of species co-occurrence (SES), and the confidence intervals to these coefficients (alpha risk = 0.1). The coefficients that the confidence intervals to the model-averaged parameter estimates do not overlap with 0 have been highlighted in bold.

SES	Coefficient	Confidence interval	
Distance	-0.00007	-0.00074	0.00061
Area	0.155	-0.301	0.610
Connectivity	0.007	-0.215	0.228
History D	-0.016	-0.360	0.328
History I	0.114	-0.593	0.821
Soil Heat Load	0.980	-4.221	6.181
Soil pH	-0.218	-1.705	1.268
Soil Multifunctionality	0.319	-0.302	0.940

Tabla S12. Model-averaged parameter estimates for each predictor for first axis of floristic composition (DCA), and the confidence intervals to these coefficients (alpha risk = 0.1). The coefficients that the confidence intervals to the model-averaged parameter estimates do not overlap with 0 have been highlighted in bold.

Axis 1 DCA	Coefficient	Confidence interval	
Distance	0.00014	-0.00023	0.00052
Area	**0.276**	**0.095**	**0.458**
Connectivity	**0.476**	**0.339**	**0.612**
History D	0.002	-0.078	0.082
History I	-0.016	-0.168	0.136
Soil Heat Load	0.182	-1.158	1.523
Soil pH	**-1.565**	**-2.408**	**-0.721**
Soil Multifunctionality	**-0.426**	**-0.590**	**-0.261**

Capítulo 6
Discusión general

A través de los cuatro capítulos experimentales que componen la presente tesis se ha tratado de profundizar en el conocimiento de los mecanismos que determinan la colonización de taludes de carretera por parte de la vegetación leñosa y en conocer las potencialidades de los márgenes de carretera como refugio y canalizadores de flujos de vegetación en ambientes fragmentados. En este capítulo de discusión general se trata de integrar las principales aportaciones obtenidas en los capítulos experimentales y ofrecer recomendaciones a las empresas y administraciones para la gestión y restauración de los márgenes de las carreteras con unos objetivos a medio y largo plazo.

Esta tesis se centra en el estudio de la vegetación perenne, que puede ser considerada una pieza fundamental en prácticamente todos los ecosistemas terrestres. Esta vegetación es reconocida como ingeniera del paisaje en muchos ecosistemas (Jones et al. 1994) y especialmente en los ecosistemas mediterráneos, dentro de los cuales se enmarca esta tesis (Bruno et al. 2003; Perelman et al. 2003; Gómez-Aparicio et al. 2004; Wilby & Shachak 2004; Luzuriaga et al. 2012). Sin embargo, pese al importante que papel que puede desempeñar este tipo de plantas, pocos estudios se habían centrado en su estudio en los márgenes de las carreteras bajo ambientes mediterráneos. Además, el estudio de la vegetación perenne permite obtener conclusiones que son independientes del momento concreto en que se realiza la toma de datos (picos fenológicos, cambios meteorológicos interanuales, etc.), y por tanto, dar unas recomendaciones más generales para la restauración y gestión de estos ecosistemas nóveles con objetivos a medio y largo plazo.

EL PAPEL DE LAS PLANTACIONES

Cuanto se trata de conocer el comportamiento de la vegetación perenne en los márgenes de carreteras, lo primero que debe analizarse es el papel de la principal medida de restauración destinada a aumentar la

cobertura leñosa en los taludes: las plantaciones. Las plantaciones en los márgenes de carretera se realizan con objetivos estéticos, de estabilización de taludes y de integración ecológica, tratando de atenuar los filtros abióticos y de favorecer la sucesión secundaria (Booth et al. 1999; Singh et al. 2002; Badía et al. 2007). Sin embargo, algunos trabajos han demostrado que los beneficios que se les atribuyen son cuestionables, tanto por utilizar individuos que pueden no estar adaptados a las duras condiciones iniciales de los taludes (Hartley 2002), como por depender de que en el entorno haya realmente dispersores que hagan esa integración ecológica con el resto del territorio (de Torre et al. 2015). Los resultados obtenidos en el Capítulo 2 de esta tesis también ponen en duda la eficacia de las plantaciones como medida de integración ecológica, ya que la presencia de vegetación plantada en los terraplenes no determina un aumento en la cantidad de cobertura total de vegetación leñosa. Además, en los Capítulos 3 y 4 se ha demostrado que la vegetación arbórea, y perenne en general, llega y se establece en los márgenes de las carreteras sin necesidad de plantaciones previas. Por tanto, esta tesis cuestiona la eficiencia de las medidas de reforestación en la restauración y la integración ecológica de las áreas afectadas por la construcción de carreteras, así como el papel de las plantaciones en el funcionamiento del ecosistema analizado a distintas escalas espaciales. Frente a las plantaciones artificiales, la colonización natural se manifiesta como un suceso suficientemente exitoso como para cumplir los objetivos asignados a la vegetación perenne.

COLONIZACIÓN NATURAL EN MÁRGENES DE CARRETERA

A lo largo de toda esta tesis se ha demostrado que la vegetación perenne es capaz de llegar y establecerse en los márgenes de las carreteras. A una escala regional amplia y ambientalmente heterogénea (Capítulo 2) se ha utilizado un muestreo extensivo para soslayar los

estudios "site-dependent" (García-Palacios et al. 2010; de Torre 2014) y eliminar los problemas de estudios con poco número de réplicas (Prach et al. 2007). De esta forma se han obtenido unos resultados que han permitido explicar, de manera generalizable, los condicionantes para la colonización de los terraplenes de carretera por parte de la vegetación leñosa. Los resultados obtenidos han permitido concluir que la colonización natural depende mucho más de factores locales, como la edad de los taludes o las características del entorno muy cercano, que de factores que actúan a escalas más amplias (clima, litología, usos del suelo, etc.). Sin embargo, dada la forma en que se ha abordó ese estudio (grandes superficies, uso de fotografías aéreas y bases de datos), en el Capítulo 2 fue imposible analizar las respuestas diferenciales que distintas especies podían tener frente a distintas características de los taludes y diferentes estructuras del paisaje en el entorno de la carretera.

Por ello, el Capítulo 3 profundiza en los factores que determinan la presencia de vegetación arbórea en taludes de carretera pero desde una perspectiva más concreta, considerando la respuesta de cada especie arbórea en distintos tipos de taludes y frente a diferentes configuraciones espaciales del paisaje. Con los resultados de este Capítulo se resalta que el comportamiento de cada especie es variable, aunque puede ser agrupado en grandes tipos dependiendo del tipo de dispersión de sus semillas. Tanto las especies con dispersión mediada por animales como las especies de dispersión por viento son capaces de llegar y establecerse de forma efectiva a los taludes. Sin embargo, las especies arbóreas de dispersión por animales, dependen en gran medida del entorno, tanto en la necesidad de tener una fuente de semillas (necesidad de presentar potenciales árboles madre en un entorno muy próximo) como en la necesidad de tener unos vectores de dispersión apropiados (estructura de la vegetación en el entorno medio o lejano). Por el contrario, las especies de árboles dispersadas por el viento depende nen mayor medida de las características de micrositio de los taludes, lo que

apunta a que no tienen una limitación importante de llegada a los taludes.

Dentro de los vectores especializados de dispersión de semillas, el hombre también puede llegar a tener un papel importante (Capítulo 3). La dispersión mediada por humanos se ha descrito en algunos casos (Wichmann et al. 2009; Pickering & Mount 2010), concretamente asociada a la presencia de semillas y propágulos en los coches (Clifford 1959; Zwaenepoel et al. 2006; Taylor et al. 2012), e incluso generando flujos de viento con los vehículos (von der Lippe et al. 2013). Además de estos mecanismos, algunas de las especies encontradas en el Capítulo 3 posiblemente han llegado a los taludes a través de semillas arrojadas por los ocupantes de los coches desde las ventanillas, por ser especies frutales de consumo humano no presentes en los entornos de la carretera.

En estos dos primeros capítulos se constata a escala regional que, pese a la existencia de fuertes condicionantes, la vegetación leñosa no presenta grandes impedimentos para llegar a los taludes de las carreteras. Más aún, en el Capítulo 4 se resalta que la llegada de especies a los márgenes de las carreteras representa a prácticamente todo el pool de especies perennes presentes en el territorio, aunque configurando unas comunidades distintas a las que se dan en los entorno naturales. Estas distintas comunidades responden fundamentalmente a los diferentes factores edáficos y constructivos propios de cada tipo de margen de carretera.

Pese a que en los tres capítulos que hemos valorado la llegada y el establecimiento de especies perennes a los márgenes de carreteras hemos encontrado que esta ha sido efectiva, también se ha detectado la existencia de ciertos filtros que este tipo de plantas tienen que atravesar. Estos filtros se agrupan en condicionantes para la llegada de semillas y disponibilidad de micrositios apropiados para el establecimiento (Münzbergová & Herben 2005). La llegada de semillas a los márgenes de la vía esta determinada por la presencia de fuentes de propágulos en el entorno, así como del comportamiento de los

vectores de dispersión, ya sean animales (Jordano & Godoy 2002; Coulson et al. 2013) o el viento (Nathan et al. 2002; Bohrer et al. 2008; Pounden et al. 2008; Schurr et al. 2008). Con esta tesis se ha demostrado que una de las principales variables para describir el comportamiento de la vegetación leñosa en los terraplenes ha sido la presencia de plantas leñosas en el entorno más próximo a la vía (Capítulo 2). Esto demuestra la gran importancia de tener la fuente de semillas muy cerca del talud. Sin embargo, en el Capítulo 3 se destaca que la presencia de árboles adultos conespecíficos muy cerca de la vía es determinante para las especies de árboles dispersadas por animales, pero no para las dispersadas por el viento. Para las especies zoócoras, estos árboles cercanos a la vía son tanto fuente de semillas, como atractores de fauna dispersora (Pausas et al. 2006; Coulson et al. 2013), función que es potenciada aún en mayor medida por la existencia de estructuras boscosas en el paisaje a mayor distancia. Para que un árbol cercano a la vía sea un atractor efectivo de dispersores (fundamentalmente aves), estos tienen que estar presentes en densidades suficientes en el entorno, lo que viene definido en gran medida por la estructura del paisaje (de Torre et al. 2015). Aún con estos condicionantes, la llegada de las especies a los márgenes de las carreteras es sólo cuestión de tiempo (Capítulo 2), lo que determina que tarde o temprano, prácticamente todas las especies perennes terminen llegando a estos ecosistemas nóveles (Capítulo 4).

La llegada de semillas no asegura la germinación y el establecimiento, sobre todo en ambientes mediterráneos donde las limitaciones ambientales (y especialmente las hídricas) son altas (Bochet & García-Fayos 2004; Tormo et al. 2006). Además del filtro hídrico, las especies han tenido que vencer otros filtros como la baja cantidad de nutrientes, los condicionantes físico-químicos, las características microclimáticas y los provocados por las interacciones bióticas planta-planta y planta-suelo (Jim 1999; Cano et al. 2002; García-Palacios et al. 2010; Mola et al. 2011; de la Riva et al. 2011; García-Palacios et al. 2011; Jiménez et al. 2011; de To-

rre 2014). Estos filtros son más o menos fuertes dependiente del tipo de margen de carretera, ya que dependiendo de sus características constructivas (Bochet & García-Fayos 2004; Jiménez et al. 2011) varía la pendiente, el sustrato/suelo, el extendido o no de tierra vegetal, etc. Todos estos filtros parecen ser determinantes en el éxito en el establecimiento de las especies de dispersión por viento (Capítulo 3). Además, las diferencias asociadas tanto al suelo como a otras características de los distintos tipos de márgenes de carretera determinan diferentes comunidades (Capítulo 4), con lo cual se genera unos ecosistemas heterogéneos a lo largo de la carretera.

Especial consideración merece la edad de los taludes desde su construcción, ya que tanto en el Capítulo 2 como en el 3 se ha descrito como una variables importante, y es un predictor que puede estar afectando tanto a los filtros de llegada de semillas como a los de establecimiento de los individuos. Por un lado, la probabilidad acumulada de que una especie alcance un margen de carretera es proporcional a la edad de este (Jacquemyn et al. 2001). Por otro lado, la capacidad de carga de un talud aumenta con el tiempo. En primer lugar, esta mejora ambiental se basa en que el establecimiento de especies pioneras influye en la fertilidad y estabilidad del suelo, lo cual suele favorecer el establecimiento posterior de especies más exigentes (García-Palacios et al. 2011; Jiménez et al. 2011). Pero también se basa en un aumento de la heterogeneidad ambiental derivada de la existencia de procesos gravitacionales en los taludes, los cuales generan zonas de erosión y de acumulación de agua, suelo y nutrientes, y por tanto dando diferente peso a los filtros de micrositio dependiendo de la zona del talud.

CONSERVACIÓN DE LA BIODIVERSIDAD Y CANALIZACIÓN DE FLUJOS ECOLÓGICOS

El alto éxito tanto en la llegada como en el establecimiento de la vegetación perenne en los márgenes de las

carreteras (Capítulos 2, 3 y 4) demuestra la existencia de flujos de especies transversales a la vía, conectando los territorios adyacentes y los taludes de las carreteras. En los Capítulos 4 y 5 se da un paso más allá, analizando no sólo los condicionantes de llegada y establecimiento, sino también las potencialidades de los márgenes de carretera como refugio de especies y como canalizadores de flujos de vegetación en un paisaje fragmentado pero de alto interés para la conservación. Los resultados han sido dispares.

Por una parte, se ha demostrado que casi todo el pool territorial de especies es capaz de llegar y establecerse en los márgenes de las vías, incluyendo especies raras, protegidas o endémicas (Capítulo 4). Este resultado apunta a que los márgenes de carretera puede considerarse un refugio y reservorio de biodiversidad, como también han demostrado otros autores (Tikka et al. 2000; Spooner & Smallbone 2009). Pero además, los márgenes de la vía no solo albergan a la mayoría de especies de su entorno, sino que también incorporan nuevas especies adaptadas a las condiciones propias de cada tipo de margen (ver también Jakobsson et al. 2016), mitigando con ello la pérdida de riqueza de especies y diversidad beta asociada a la intensificación agraria (Benton et al. 2003; Strijker 2005; Karp et al. 2012).

El papel de refugio y reservorio de diversidad asignado a los márgenes de carretera (Capítulo 4; Tikka et al. 2000; Spooner & Smallbone 2009; Jakobsson et al. 2016), así como los flujos de vegetación perpendiculares y paralelos a la vía demostrados en muchos estudios (Capítulos 2, 3 y 4; Tikka et al. 2001; Bochet et al. 2007; de la Riva et al. 2011; Smit & Asner 2012; von der Lippe et al. 2013; Auffret & Cousins 2013) apuntan a una interconexión entre los márgenes de la carretera y los remanentes de hábitat del paisaje fragmentado (Capítulo 5). Teniendo en cuenta los resultados obtenidos y la bibliografía se esperaba encontrar que la distancia a la carretera de los remanentes de hábitat fuera un predictor importante para explicar las características estructurales y funcionales de las comunidades de plantas perennes

de dichos remanentes. Sin embargo, no se ha encontrado ningún efecto significativo de la distancia a carretera sobre dichas comunidades en los remanentes de hábitat cercanos a la vía. Con ello no se descarta que existan dicho efectos, sino que pueden estar ocurriendo a unas escalas espaciales distintas a las utilizadas en esta tesis, o manifestándose como respuestas de umbrales más que como gradientes continuos de distancias. En este sentido son necesarios estudios más específicos para realmente estimar la contribución neta de dichos efectos y los condicionantes para que sean efectivos.

RESTAURACIÓN PASIVA COMO HERRAMIENTA PARA LOS PROFESIONALES

Los resultados de esta tesis permiten afirmar que la restauración pasiva puede llegar a ser una poderosa herramienta de restauración ecológica de los márgenes de las carreteras siempre que se den las condiciones idóneas tanto en el propio margen como en el entorno cercano. Por tanto, para potenciar la restauración pasiva de estos ecosistemas nóveles, los resultados de esta tesis plantean dos líneas de actuación. Por un lado, se puede actuar a nivel de los propios márgenes para que las semillas y propágulos que lleguen encuentren micrositios favorables para su establecimiento. Esta línea es sobre la que tradicionalmente se ha hecho más hincapié, actuando sobre los componentes geomorfológicos (por ejemplo, pendiente del talud), edáficos (por ejemplo, aportes de tierra vegetal) o biológicos (por ejemplo, plantaciones e hidrosiembras) del sistema. Por otro lado, la actuación puede realizarse a nivel de los entornos más cercanos, conservando en ellos la vegetación natural y su capacidad de dispersión. En la construcción de una nueva infraestructura o en la gestión durante la fase de funcionamiento, parece más interesantes conservar remanentes de vegetación natural cercanos a los márgenes de la carretera, que gastar dinero en plantaciones.

La restauración pasiva realizada bajo estas premisas tiene capacidad de mejorar la conservación de la diver-

sidad biológica en ambientes agrícolas, ya que mantiene el pool regional de especies y permite que se establezcan flujos ecológicos entre los márgenes de las carreteras y sus entornos. Además, también ayuda a minimizar los costes de mantenimiento de las carreteras, reduciendo los pasivos ambientales para las empresas y gobiernos que mantienen las infraestructuras. Sin embargo, la restauración pasiva requiere tiempo y necesita conjugar los objetivos técnicos a corto plazo, principalmente disminuir la erosión para no comprometer la estabilidad de la vía, con los objetivos de restauración ecológica a medio y largo plazo, focalizados en obtener beneficios ambientales como la conservación de la biodiversidad o la mejora de algunos servicios ecosistémicos debilitados. Por tanto, los esfuerzos se deben orientar hacia el desarrollo de planes de restauración que combinen los objetivos planteados a diferentes escalas espaciales y temporales.

BIBLIOGRAFÍA

Auffret, A.G., & Cousins, S.A.O. 2013. Grassland connectivity by motor vehicles and grazing livestock. *Ecography* 001–008.

Badía, D., Valero, R., Gracia, A., Martí, C., & Molina, F. 2007. Ten-year growth of woody species planted in reclaimed mined banks with different slopes. *Arid Land Research and Management* 21: 67–79.

Benton, T.G., Vickery, J. A., & Wilson, J.D. 2003. Farmland biodiversity: Is habitat heterogeneity the key? *Trends in Ecology and Evolution* 18: 182–188.

Bochet, E., & García-Fayos, P. 2004. Factors Controlling Vegetation Establishment and Water Erosion on Motorway Slopes in Valencia, Spain. *Restoration Ecology* 12: 166–174.

Bochet, E., García-Fayos, P., & Tormo, J. 2007. Road slope revegetation in semiarid Mediterranean environments. Part I: seed dispersal and spontaneous colonization. *Restoration Ecology* 15: 88–96.

Bohrer, G., Katul, G.G., Nathan, R., Walko, R.L., & Avissar, R. 2008. Effects of canopy heterogeneity, seed abscission and inertia on wind-driven dispersal kernels of tree seeds. *Journal of Ecology* 96: 569–580.

Booth, D., Gores, J., Schuman, G., & Olson, R. 1999. Shrub densities on pre-1985 reclaimed mine lands in Wyoming. *Restoration Ecology* 7: 24–32.

Bruno, J.F., Stachowicz, J.J., & Bertness, M.D. 2003. Inclusion of facilitation into ecological theory. *Trends in Ecology and Evolution* 18: 119–125.

Cano, A., Navia, R., Amezaga, I., & Montalvo, J. 2002. Local topoclimate effect on short-term cutslope reclamation success. *Ecological Engineering* 18: 489–498.

Clifford, H.T. 1959. Seed Dispersal by Motor Vehicles. *Journal of Ecology* 47: 311–315.

Coulson, C., Spooner, P.G., Lunt, I.D., & Watson, S.J. 2013. From the matrix to roadsides and beyond: the role of isolated paddock trees as dispersal points for invasion. *Diversity and Distributions* 20(2): 137-148.

García-Palacios, P., Bowker, M.A., Maestre, F.T., Soliveres, S., Valladares, F., Papadopoulos, J., & Escudero, A. 2011. Ecosystem development in roadside grasslands: biotic control, plant-soil interactions, and dispersal limitations. *Ecological applications* 21: 2806–21.

García-Palacios, P., Soliveres, S., Maestre, F.T., Escudero, A., Castillo-Monroy, A.P., & Valladares, F. 2010. Dominant plant species modulate responses to hydroseeding, irrigation and fertilization during the restoration of semiarid motorway slopes. *Ecological Engineering* 36: 1290–1298.

Gómez-Aparicio, L., Zamora, R., Gómez, J.M., Hódar, J.A., Castro, J., & Baraza, E. 2004. Applying plant facilitation to forest restoration: a meta-analysis of the use of shrubs as nurse plants. *Ecological Applications* 14: 1128–1138.

Hartley, M. 2002. Rationale and methods for conserving biodiversity in plantation forests. *Forest Ecology and Management* 155: 81–95.

Jacquemyn, H., Butaye, J., Dumortier, M., Hermy, M., & Lust, N. 2001. Effects of age and distance on the composition of mixed deciduous forest fragments in an agricultural landscape. *Journal of Vegetation Science* 12: 635–642.

Jakobsson, S., Fukamachi, K., & Cousins, S.A.O. 2016. Connectivity and management enables fast recovery of plant diversity in new linear grassland elements. *Journal of Vegetation Science* 27: 19–28.

Jim, C. 1999. A planning strategy to augment the diversity and biomass of roadside trees in urban Hong Kong. *Landscape and Urban Planning* 44: 13–32.

Jiménez, M.D., Ruíz-Capillas, P., Mola, I., Pérez-Corona, E., Casado, M.A., & Balaguer, L. 2011. Soil development at the roadside: a case study of a novel ecosystem. *Land Degradation & Development & Development* 24: 564–574.

Jones, C., Lawton, J., & Shachak, M. 1994. Organisms as ecosystem engineers. *Ecosystem Management* 69: 373–386.

Jordano, P., & Godoy, J. 2002. The dynamics of frugivore- generated seed shadows: demographic and genetic effects. In Levey, D.J., Silva, W., & Galetti, M. (eds.), *Seed dispersal and frugivory: ecological, evolutionary, and conservation*, pp. 305–321. CABI Publishing, Wallingford.

Karp, D.S., Rominger, A.J., Zook, J., Ranganathan, J., Ehrlich, P.R., & Daily, G.C. 2012. Intensive agriculture erodes ß-diversity at large scales. *Ecology Letters* 15: 963–970.

de la Riva, E.G., Casado, M.A., Jiménez, M.D., Mola, I., Costa-Tenorio, M., & Balaguer, L. 2011. Rates of local colonization and extinction reveal different plant community assembly mechanisms on road verges in central Spain. *Journal of Vegetation Science.* 22: 292–302.

von der Lippe, M., Bullock, J.M., Kowarik, I., Knopp, T., & Wichmann, M. 2013. Human-mediated dispersal of seeds by the airflow of vehicles. *PloS One* 8: e52733.

Luzuriaga, A.L., Sánchez, A.M., Maestre, F.T., & Escudero, A. 2012. Assemblage of a semi-arid annual plant community: abiotic and biotic filters act hierarchically. *PloS one* 7: e41270.

Mola, I., Jiménez, M.D., López-Jiménez, N., Casado, M. A., & Balaguer, L. 2011. Roadside Reclamation Outside the Revegetation Season: Management Options under Schedule Pressure. *Restoration Ecology* 19: 83–92.

Münzbergová, Z., & Herben, T. 2005. Seed, dispersal, microsite, habitat and recruitment limitation: identification of terms and concepts in studies of limitations. *Oecologia* 145: 1–8.

Nathan, R., Horn, H.S., Chave, J., & Levin, S.A. 2002. Mechanistic models for tree seed dispersal by wind in dense forests and open landscapes. In Levey, D.J., Silva, W.R., & Galetti, M. (eds.), *Seed dispersal and frugivory: Ecology, Evolution and Conservation*, pp. 69–82. CABI Publishing, Wallingford, Oxon, UK.

Pausas, J.G., Bonet, A., Maestre, F.T., & Climent, A. 2006. The role of the perch effect on the nucleation process in Mediterranean semi-arid oldfields. *Acta Oecologica* 29: 346–352.

Perelman, S.B., Burkart, S.E., & León, R.J.C. 2003. The role of a native tussock grass (Paspalum quadrifarium Lam.) in structuring plant communities in the Flooding Pampa grasslands, Argentina. *Methods* 12: 225–238.

Pickering, C., & Mount, A. 2010. Do tourists disperse weed seed? A global review of unintentional human-mediated terrestrial seed dispersal on clothing, vehicles and horses. *Journal of Sustainable Tourism* 18: 239–256.

Pounden, E., Greene, D.F., Quesada, M., & Contreras Sánchez, J.M. 2008. The effect of collisions with vegetation elements on the dispersal of winged and plumed seeds. *Journal of Ecology* 96: 591–598.

Prach, K., Pysek, P., & Jarosík, V. 2007. Climate and pH as determinants of vegetation succession in Central European man-made habitats. *Journal of Vegetation Science* 18: 701–710.

Schurr, F., Steinitz, O., & Nathan, R. 2008. Plant fecundity and seed dispersal in spatially heterogeneous environments: models, mechanisms and estimation. *Journal of Ecology* 96: 628–641.

Singh, A.N., Raghubanshi, A.S., & Singh, J.S. 2002. Plantations as a tool for mine spoil restoration. *Current Science* 82: 1436–1441.

Smit, I.P.J., & Asner, G.P. 2012. Roads increase woody cover under varying geological, rainfall and fire regimes in African savanna. *Journal of Arid Environments* 80: 74–80.

Spooner, P., & Smallbone, L. 2009. Effects of road age on the structure of roadside vegetation in South-eastern Australia. *Agriculture, Ecosystems & Environment* 129: 57–64.

Strijker, D. 2005. Marginal lands in Europe - Causes of decline. *Basic and Applied Ecology* 6: 99–106.

Taylor, K., Brummer, T., Taper, M.L., Wing, A., & Rew, L.J. 2012. Human-mediated long-distance dispersal: an empirical evaluation of seed dispersal by vehicles. *Diversity and Distributions* 18: 942–951.

Tikka, P., Högmander, H., & Koski, P. 2001. Road and railway verges serve as dispersal corridors for grassland plants. *Landscape ecology* 16: 659–666.

Tikka, P., Koski, P., Kivelä, R., & Kuitunen, M. 2000. Can grassland plant communities be preserved on road and railway verges? *Applied Vegetation Science* 3: 25–32.

Tormo, J., Bochet, E., & García-fayos, P. 2006. Is seed availability enough to ensure colonization success?An experimental study in road embankments. *Ecological Engineering* 26: 224–230.

de Torre, R. 2014. Procesos ecologicos en el emsamblaje de comunidades en taludes de carretera y su aplicacion en la restauracion ecologica.

de Torre, R., Jiménez, M.D., Ramírez, Á., Mola, I., Casado, M.A., & Balaguer, L. 2015. Use of restoration plantings to enhance bird seed dispersal at the roadside: failures and prospects. *Journal of Environmental Engineering and Landscape Management* 23: 302–311.

Wichmann, M.C., Alexander, M.J., Soons, M.B., Galsworthy, S., Dunne, L., Gould, R., Fairfax, C., Niggemann, M., Hails, R.S., & Bullock, J.M. 2009. Human-mediated dispersal of seeds over long distances. *Proceedings. Biological sciences / The Royal Society* 276: 523–532.

Wilby, A., & Shachak, M. 2004. Shrubs, granivores and annual plant community stability in an arid ecosystem. *Oikos* 106: 209–216.

Zwaenepoel, A., Roovers, P., & Hermy, M. 2006. Motor vehicles as vectors of plant species from road verges in a suburban environment. *Basic and Applied Ecology* 7: 83–93.

Conclusiones generales

De los cuatro capítulos experimentales de los que consta esta tesis (capítulos 2, 3, 4 y 5) se pueden extraer las siguientes conclusiones generales:

I. La vegetación leñosa de gran porte es capaz de llegar y establecerse de manera eficaz en los terraplenes de las autovías. La llegada de semillas de este tipo de plantas se realiza de forma efectiva mediante colonización natural desde los entornos próximos.

II. Las plantaciones en los taludes, a las que se les atribuye un efecto de fuente de semillas y de atractor de especies dispersoras, no sólo no aceleran el desarrollo de la vegetación leñosa en terraplenes sino que incluso podrían tener un efecto negativo.

III. Existe un patrón general para explicar la colonización de la vegetación leñosa en terraplenes. El éxito en la colonización depende tanto de las características del talud, principalmente su edad, como de la vegetación circundante más cercana. Cuando la vegetación circundante a los taludes mantiene buenas condiciones y las características de los taludes son apropiadas, la restauración pasiva es una buena herramienta para favorecer el establecimiento de la vegetación leñosa en taludes.

IV. Las medidas de conservación de las áreas con vegetación leñosa cercanas a la vía durante la fase de construcción de las carreteras son críticas para la colonización posterior de los terraplenes por parte de dicha vegetación leñosa.

V. Un alto número de especies arbóreas son capaces de llegar y establecerse en taludes de carretera bajo configuraciones del paisaje y características de micrositio muy diferentes. Tanto las especies dispersadas por viento, como las especies de dispersión por animales se establecen en los taludes de carretera a través de la colonización natural.

VI. Las especies arbóreas dispersadas por el viento tienen pocas limitaciones para la llegada a los taludes, pudiendo estar ausentes en el entorno más próximo de los taludes. Sin embargo, para su desarrollo requieren de condiciones muy específicas a escala de micrositio.

VII. Las especies arbóreas de dispersión mediada por animales son ecológicamente más demandantes ya que necesitan árboles adultos conespecíficos cerca de los taludes, dispersores en el entorno y tiempo suficiente para la llegada y el establecimiento. Este tiempo no es superior los 20 años.

VIII. El comportamiento ecológico de las diferentes especies arbóreas condiciona las medidas de restauración enfocadas en promover su colonización natural en taludes. Las especies zoócoras requieren que el foco se centre en la calidad del hábitat cercano, mientras que para las especies anemócoras el foco debe centrarse en las características del micrositio. Por tanto, los planes de restauración basados en promover la colonización natural pueden, y deben, basarse en grupos de especies y no tanto en especies aisladas.

IX. Los márgenes de carretera albergan una comunidad de plantas perennes bien establecida y diversa, pero diferenciada de la vegetación natural de sus entornos próximos. Estas diferencias vienen dadas fundamentalmente por las distintas condiciones edáficas.

X. La gran mayoría de las especies que aparecen en la vegetación natural cercana a una carretera se encuentran en los márgenes de la vía. Por tanto, estos ecosistemas noveles son excelentes reservorios de diversidad, albergando muchas especies interesantes desde el punto de vista de la conservación, incluyendo tanto especies raras en el entorno como protegidas o endémicas.

XI. Las comunidades gipsófilas de remanentes de hábitat en un ecosistema agrícola fragmentado y atravesado por una autovía se organizan atendiendo a variables que actúan tanto a escala local (edáficas) como a escala de paisaje. Los predictores a escala de paisaje afectan en último término y de forma indirecta a la calidad del suelo.

XII. Para la conservación efectiva de la flora protegida en ambientes gipsófilos fragmentados es necesario conservar al área central de los fragmentos, reducir el efecto borde y limitar las actividades que degraden el suelo. A su vez, la restauración ecológica de los fragmentos degradados debería focalizarse en recuperar las características del suelo para recuperar comunidades típicas de yesos, sin descuidar mejoras en la conectividad que aumenten la funcionalidad y resiliencia a escala de paisaje.

XIII. No se han encontrado efectos positivos o negativos de las carreteras sobre la comunidad gipsófila en fragmentos de hábitat cercanos a la vía. Sin embargo, teniendo en cuenta la escala y los condicionantes de diseño con los que se ha realizado este estudio concreto, son necesarios más estudios para poder asegurar esa carencia de efecto.

Agradecimientos

Este largo proceso está llegando a su fin. Quién me lo iba a decir en los innumerables bajones que he tenido. Bueno sí, me lo decían todas las personas que de una manera o de otra me habéis dado el empujón necesario para continuar. Esto no hubiera sido posible sin todo el apoyo humano que he tenido.

En primer lugar quiero agradecer a mis directores. Del primero que me quiero acordar es de Luis Balaguer, sin él y su maravillosa e inigualable asignatura de Restauración de la cubierta vegetal de la Licenciatura en Biología, yo dudo que me hubiera planteado hacer una tesis, pero lo que tengo seguro es que no la hubiera hecho en Restauración de taludes carreteras, que lo asumo, no es el lugar idílico donde muestrear. Una vez acabada la tesis, he de decir que repetiría escenarios una y mil veces. Me jode (perdón) mucho, que Luis no pueda estar físicamente aquí, aunque estar está en esta tesis y en muchos más sitios, porque Luis es Eterno. Luis un día me dijo: "¿Seguro que quieres pedir una tesis conmigo? Posiblemente no me queden más de 6 meses de vida", Mi respuesta fue: "A mí me puede atropellar un camión esta misma tarde, así que vamos para adelante". Luis me enseño que hay que luchar hasta el último día. Gracias Luis, para mí siempre serás un referente.

En pleno proceso para solicitar mi beca FPU, Luis me planteó que él iba a firmar otra solicitud y que por temas legales solo podía firmar una al año, pero que había estado hablando con otro profesor que consideraba que podría ser muy buen director y que él me podría firmar la solicitud. Al decirme el nombre solo pude sonreír, era Miguel Ángel Casado. Miguel era, junto a Luis, de los mejores profesores que había tenido en la carrera. De esos profesores que igual están en el monte hablándote de unos procesos geomorfológicos, que de una planta, que con un papel y un boli enseñándote estadística cual matemático. Yo quería ser como él, y mira por donde, iba a ser mi director de Tesis. Durante estos años no he llegado aún a ser como él, pero he aprendido lo máximo posible y he disfrutado muchísimo compartiendo muestreos de campo, reuniones y horas de oficina. Además, si tengo claro que sin Luis nunca hubiera empezado esta tesis, más claro aun tengo que sin Miguel no la hubiera acabado, y no solo por su incalculable aporte científico, que ha conseguido que todos los artículos que he enviado hayan sido aceptados en el primer intento, sino por esa calma que te transmite justo cuando más necesitas tranquilidad y serenidad para continuar. Miguel, tras estos años, me reafirmo

en eso que pensé en la carrera y repito: "de mayor quiero ser como tú".

Mi tercer director no empezó siéndolo, aunque si estaba en el proyecto. Pero tras el fallecimiento de Luis, Adrián Escudero tomó ese papel de codirector tan necesario. Un investigador como él sin duda ha enriquecido muchísimo esta tesis, y junto a Miguel, es el culpable de que los artículos hayan entrado a las primeras revistas a las que se han enviado. Pero una persona que firma sus correos como "eladri" y que en verano se deja pintar las uñas de los pies por su hija, no puede ser solo un apoyo científico. Sus ánimos para continuar y superar los bajones anímicos han sido decisivos para sacar fuerzas, muchos veces no sé de donde. Adri, si un día mi hijo me quiere pintar las uñas de los pies de verde, no dudes que lo haré, ya que un Grande las llevaba así.

Formalmente mi tesis tiene tres directores, pero sentimentalmente tiene cuatro. Sin duda, Iñaki Mola para mí es mi cuarto director. Iñaki, era el hombre de la empresa en el grupo, y el encargado de conseguir un proyecto para mi tesis. Pero Iñaki ha sido muuuuucho más, de él he aprendido muchísimo sobre construcción de carreteras y junto a él he compartido muchos de los muestreos de campo, gazpacho andaluz incluido, con todo lo que ello conlleva, ya que en el campo no solo se muestrea sino que se aprende. Además de que sin él, las identificaciones de plantas me hubieran torturado. Pero la contribución de Iñaki no se reduce al aporte técnico. Su mayor contribución a esta tesis, se produjo en un solo día, pero que he recordado cada día durante el resto de la tesis. Durante el primer bajón importante que tuve con la tesis, y posiblemente el más gordo, Iñaki me "puso su hombro" para que me desahogara y después me recargó las pilas. Ese "hombro" y esa conversación salvaron mi tesis en ese momento y en muchos momentos posteriores. Esta tesis no hubiera sido posible sin ese rumbo, esa dirección, que me marcó Iñaki ese día. Iñaki, muchas gracias por ese y por tanto otros días que hemos pasado juntos durante esta tesis.

A las siguientes a las que agradecer, es a mis "hermanas Obviusly", Sandra y Rocío. Junto a ellas, o gracias a ellas, descubrí lo que era muestrear en taludes y lo que es hacer una tesis en Restauración de taludes de carretera. Me marcaron el camino a seguir. Sus aportes científicos, ayudas en congresos, sus cigarros (yo creo que al final se dieron cuenta de que yo no fumaba, por mucho que les dijera ¿fumamos?), sus consejos (Rocío, a "Polite" no te gana nadie y algo he intentado aprender, aunque me cuesta...), sus

ánimos ante los bajones y un largo etcétera hacen de ellas... no unas compañeras, sino "mis hermanas mayores de la ciencia". Rocío, Sandra, ¡muchas gracias!

Y como no acordarme de la otra sección "Obviusly", los del "Comando Acebuche", Agus, Adri y Peri, que también aportaron consejos científicos y ratos de desconexión. Agus y esas eternas conversaciones hablando de ciencia, o de no ciencia, que fiestas también hemos tenido algunas. Adri, no mires para otro lado que tú también estabas ahí. Peri, tú eras eso que yo quería ser, un doctorando acabando una tesis y con una solvencia estadística envidiable, aunque el último día casi me matas. Y por supuesto, un hueco especial para Ana, nuestra "tecno-secre". ¡¡Qué hubiéramos hecho sin ti!! No quiero olvidarme del resto de compañeros del grupo y de la complutense: Mariló, Juan, Quique, Irene, Irene, Sara B, Sara C, Dolores, Monika, Fernando... (seguro que me dejo gente, ¡perdón!) que han colaborado en los diseños y muestreos, me han ayudado a crecer como investigador y me han dado ratos de desconexión muy necesarios. Y también una mención a los "Juancarlinos", en especial a Laura y a Jesús.

Dando una visión a más largo plazo, veo a mis amigos del final de la carrera. Esos que con una cerveza de máquina en forestales, hicieron que me interesara por el mundo de la ciencia. Gracias a ellos empecé a ver que tras un largo día de clases, me seguía apeteciendo seguir por la universidad hablando de lo mismo. Y aunque no de nombres, no puedo no nombrar a Miguel, a Álvaro y a Cornejo, ya que no solo estaban en esas cervezas, sino que han seguido todo este tiempo apoyándome de una u otra manera. Patri, que sí, que también me acuerdo de ti, pero es que tú no estabas en la máquina de cervezas.

Tras la carrera, llegó el Máster de Restauración de Ecosistemas. Donde adquirí conocimientos muy necesarios para el desarrollo de esta tesis, ya que la mayoría de profesores era de un nivel excepcional. Además mis compañeros de máster hicieron mucho más agradable seguir aprendiendo día a día en clases, salidas de campo y largos trabajos que tuvimos que hacer. Gracias Carlos, Rodri, Dani, Ivan, Ivan, Olatz y al resto de compañeros.

Y hablando del Máster de Restauración, ese máster me vinculó académicamente a la Universidad de Alcalá. Donde está una de las mejores personas que me he encontrado en este proceso, una persona que te soluciona cualquier duda o papeleo de urgencia

*A veces la dificultad de la pendiente no nos deja ver
que seguimos progresando y subiendo.*

Albert Espinosa